PALEOCENE TURTLES FROM THE AQUIA AND BRIGHTSEAT FORMATIONS, WITH A DISCUSSION OF THEIR BEARING ON SEA TURTLE EVOLUTION AND PHYLOGENY

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Abstract.—The Piscataway Member of the Aquia Formation (upper Paleocene: Thanetian) has yielded remains of six species of turtles: *Aspideretes virginianus* (Clark), *Planetochelys savoiei* (n. gen., n. sp.), *Osteopygis roundsi* (n. sp.), *Dollochelys coatesi* (n. sp.), *Catapleura ruhoffi* (n. sp.), and *Allopleuron insularis* (Cope). The Brightseat Formation (lower Paleocene: Danian) has yielded three taxa: *Taphrosphys sulcatus* (Leidy), *Agomphus* sp., and *Osteopygis emarginatus* Cope. These faunas, when compared with Late Cretaceous and early Eocene marine turtle faunas, provide valuable insights into the evolutionary history of sea turtles from Late Cretaceous through Early Tertiary time. No catastrophic terminal Cretaceous extinction event among sea turtles is indicated by this succession. Rather, strong decline in the late Campanian is followed by modest recovery in the Thanetian and Ypresian. This decline and renaissance closely matches the global pattern of oceanic cooling and warming in Late Cretaceous–early Tertiary time.

Turtle remains have been reported from the Aquia Formation of the Pamunkey Group since 1895, but mostly from isolated fragments (for example, see Clark & Martin 1901). Not until Lynn (1929) described a fairly complete carapace of "*Amyda*" *virginiana* was there sufficient material adequate to characterize even one species. Even so, Lynn did not demarcate the suture boundaries on this specimen and the published illustration does not show them clearly. Since the publication of Lynn's paper, more chelonian material has turned up sporadically both in the Aquia Formation and in the underlying Brightseat Formation, but it has not been described. This new material, although far from ideal, is still sufficient to expand greatly our knowledge of the diversity and taxonomy of the turtles of Paleocene age and sheds new light on their anatomy.

Age of the Aquia and Brightseat Formations.—The Aquia formerly was considered to be a lower Eocene unit (Clark & Martin 1901), but Loeblich & Tappan (1957) demonstrated that it should properly be considered part of the upper Paleocene column on the basis of its contained planktonic Foraminifera. Greater refinement in the stratigraphic position of this unit has been achieved by Gibson and others (1980), whose work indicated that the entire Aquia lies within calcareous nannoplankton zones NP5 through NP9. The Aquia is divided into two members (Clark & Martin 1901), a lower member named the Piscataway which lies within NP5 through NP8, and an upper member named the Paspotansa which falls entirely within NP9. This division implies that the Piscataway accumulated 60 to 57 Ma and the Paspotansa accumulated 57 to 55 Ma (Fig. 1). Both members of the Aquia belong within the Thanetian Stage of the Paleocene (Hardenbol & Berggren 1978).
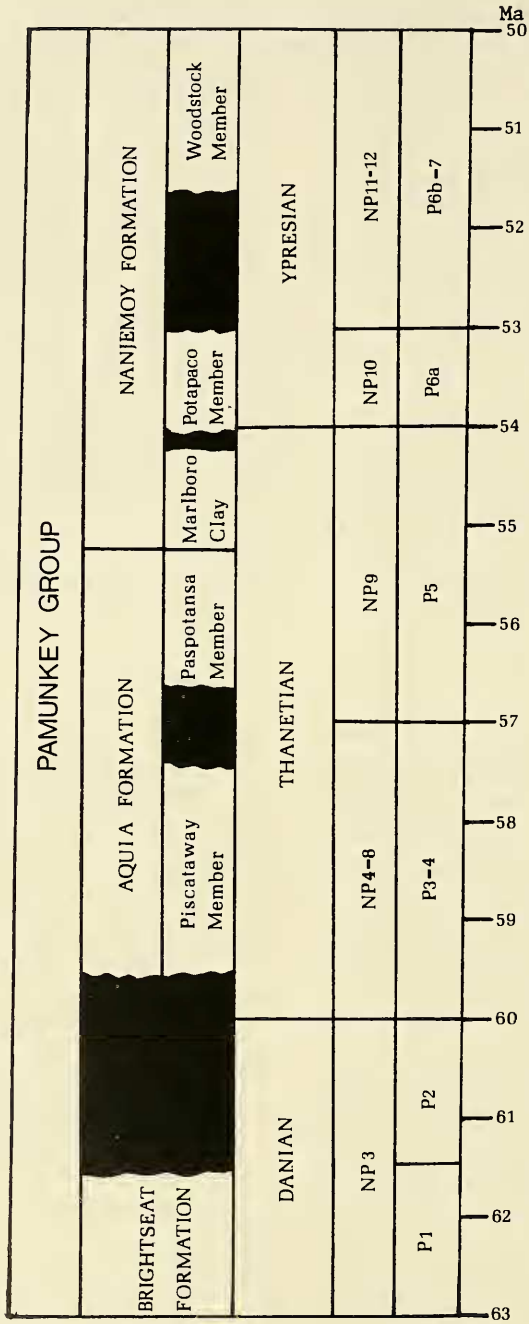
Fig. 1.   Age ranges of the members and formations comprising the Pamunkey Group in Maryland and Virginia (after Clark & Martin 1901, Gibson et al. 1980).

The Piscataway is richer in vertebrate remains than the Paspotansa, but both members are productive. All of the specimens described here from the Aquia Formation were found in outcrops of the Piscataway Member, within the outcrop belt of the Pamunkey Group (Fig. 2). There is no strong evidence from these occurrences to suggest that any of these turtles is restricted to only a part of this member. Since turtle remains have not been reported from the overlying Paspotansa Member, it is premature to say anything about the possible younger range limit for these species.

The underlying Brightseat Formation has yielded three recognizable turtle taxa. These are also known from a stratigraphically equivalent unit in New Jersey, the Hornerstown Sand. The Hornerstown has yielded a diverse, but poorly known, turtle fauna. Even so, the remains from the Hornerstown are complete enough to indicate that most of them differ from the Piscataway turtles at the species level or higher. The Brightseat, now recognized as a separate stratigraphic entity (Bennet & Collins 1952), was tentatively lumped with the Aquia as "Zone 1" by Clark & Martin (1901). It is now considered to be distinctly older (Danian) and known to have an invertebrate fauna and flora distinctly different from those found in the Aquia. In the past, the New Jersey equivalent of the Brightseat (the Hornerstown) often was regarded as Late Cretaceous in age, but this designation is no longer considered to be valid. Increasing refinement in the definition of the Cretaceous–Tertiary boundary has clearly put both the Brightseat and the Hornerstown within the Danian (Hazel 1969, Loeblich & Tappan 1957).

Within the Pamunkey Group, the only described species of turtle has been "*Trionyx*" *virginianus* (Clark 1895, 1896) from beds later known as the Piscataway Member of the Aquia. This species was transferred to *Amyda* (=*Trionyx*) by Lynn (1929), but its status was not changed otherwise. Elsewhere in the Atlantic Coastal Plain, Paleo-

Table 1.—Stratigraphic occurrences of type specimens of sea turtles described from the uppermost Cretaceous, Paleocene, and lower Eocene beds of the New Jersey Coastal Plain. *Atlantochelys mortoni,* from the greensands of Burlington County, is too vaguely referenced to be put in a specific stratigraphic unit but almost certainly came from either the Navesink (Upper Cretaceous) or Hornerstown (lower Paleocene). Locality data from Hay (1908) was sufficient to place other type specimens in specific units (J. P. Owens, oral communication 1984). *Peritresius ornatus* (=*Taphrosphys nodosus*) is known only from horizons lower than those shown here (Red Bank Formation and Navesink Formation) (Baird 1964). Stratigraphy after Minard and others (1969) and Owens & Sohl (1969); however Olsson (1963) and Gaffney (1975a) present an alternative view considering basal Hornerstown (and most of the Hornerstown vertebrate fossils) to be latest Maastrichtian in age.

Age	Unit	Holotype of:
Early Eocene	Manasquan Formation	*Chelonia parvitecta* *Lembonax polemicus* *Lembonax propylaeus*
Late Paleocene	Vincentown Formation	*Lembonax insularis* *Rhetechelys platyops*
Early Paleocene	Hornerstown Sand	*Osteopygis emarginatus* *Osteopygis gibbi* *Osteopygis robustus* *Osteopygis chelydrinus* *Osteopygis erosus* *Osteopygis borealis* *Osteopygis platylomus* *Catapleura repanda* *Catapleura ponderosa* *Lytoloma angusta* *Lytoloma jeanesi* *Lytoloma wielandi* (partly equals *Dollochelys atlantica*) *Erquelinnesia molaria*
Late Cretaceous	Tinton Sand	*Osteopygis sopitus*

cene turtles have been described only from New Jersey. No amydid turtles remotely resembling "*Amyda virginiana*" have been reported in that state from the Paleocene, but a number of chelonioid species were described from the "greensand beds." These taxa were summarized by Hay (1908) and variously allotted to "Cretaceous greensands" and "Eocene greensands." It is now
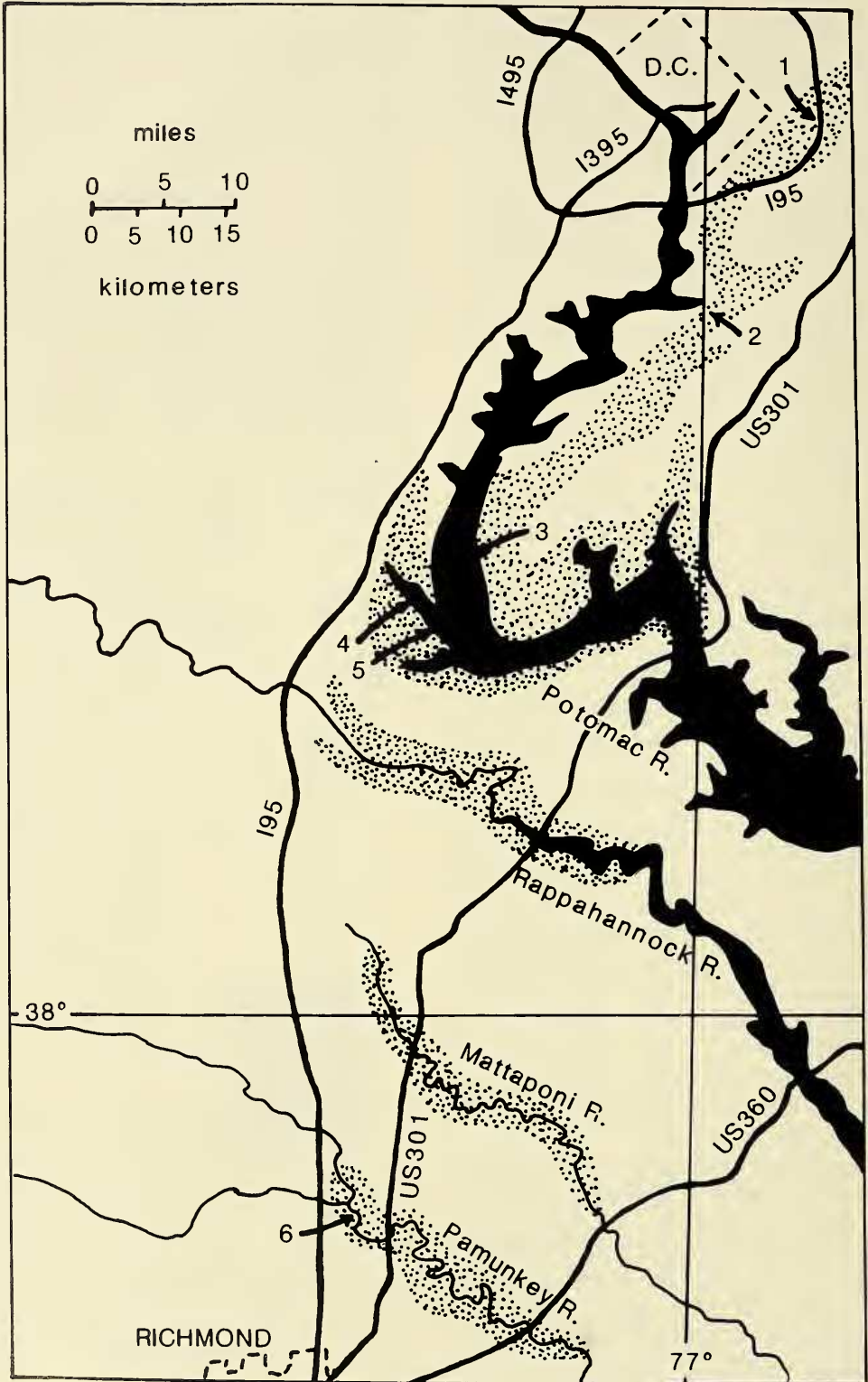
known that parts of these greensands are actually Paleocene, and, for this reason, Table 1 relates the type specimens of these New Jersey species to the modern stratigraphic terms for the units from which they came. All of the "species" of *Osteopygis* (and *Erquelinnesia molaria*) have been combined into the single species *O. emarginatus* by Zangerl (1953), who considered all of these forms to be age and individual variants within a single population. I am inclined to agree with his conclusions and suspect that "*Catapleura ponderosa*" and "*Lytoloma angusta*" (at least the jaw) may also prove to be junior synonyms of *O. emarginatus*. All of these specimens were found in what is now known as the Hornerstown Sand of the Rancocas Group of early Paleocene (Danian) age and are of approximately the same age. The one possible exception is the type specimen of "*Osteopygis sopitus*" which came from an older horizon (the Upper Cretaceous Tinton Sand) than any of the other synonymized taxa. The type is too fragmentary to determine most of the anatomy of this turtle; therefore future collecting might show that it is a valid separate species from *O. emarginatus*.

As Hay (1908) pointed out, *Lembonax polemicus* and *L. propylaeus* came from a single horizon and locality and may well represent a single species or even individual. *Lembonax insularis*, which comes from a lower horizon that is stratigraphically equivalent to the Paspotansa Member of the Aquia Formation, probably represents a distinct species. Of the remaining forms, *Rhetechelys platyops* is most distinctive. *Atlantochelys mortoni* (which cannot be clearly assigned to a unit), "*Chelonia*" *parvitecta,* and *Catapleura repanda* are fragmentary but probably diagnostic. The jaw elements referred by Hay (1908) to his species "*Lytoloma wielandi*" were later referred by Zangerl (1953) to *Osteopygis emarginatus*. As Hay had specifically designated the type of "*L. wielandi*" to be one of the jaw elements, the carapace was left apparently unnamed. To this carapace, Zangerl (1953) gave the name *Toxochelys atlantica*. Later, Zangerl (1971) erected the genus *Dollochelys*, using *D. casieri* from France as the type species, and referred his species *atlantica* to this genus.

Thus only three chelonioid species (*Catapleura repanda, Dollochelys atlantica,* and *Osteopygis emarginatus*) may be present in the lower Paleocene Hornerstown Sand. The upper Paleocene Vincentown Formation has yielded *Lembonax insularis* and *Rhetechelys platyops;* the lower Eocene Manasquan Formation has yielded *Lembonax polemicus* (=*L. propylaeus*?) and "*Chelonia*" *parvitecta*. Because these species are found so close to the Maryland-Virginia area, many will be mentioned in the following discussion.

Turtles from the Brightseat Formation

Family Pelomedusidae
Taphrosphys sulcatus (Leidy)
Fig. 3D, E

Referred specimen. —USNM 357714, fragment of a carapace including the supra-

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Fig. 2. Map showing general localities from which the turtles described in this report were excavated. Shaded areas are outcrop belts of the Pamunkey Group. 1, Hampton Mall, Maryland, at intersection of Central Avenue and Interstate 95 (reference locality for *Taphrosphys sulcatus, Agomphus* sp., and *Osteopygis emarginatus*); 2, Piscataway Creek, Maryland, at Indian Head Highway bridge (type locality for *Catapleura ruhoffi*); 3, Liverpool Point, Maryland (type locality for *Dollochelys coatesi* and reference locality for *Osteopygis roundsi*); 4, Aquia Creek bluffs, Virginia, (upper end) where "Zone 2" of Clark & Martin (1901) is exposed (type locality for *Planetochelys savoiei*); 5, Aquia Creek bluffs, Virginia, (lower end) where "Zone 6" of Clark & Martin (1901) is accessible (type area for *Aspideretes viginianus*); 6, Pamunkey River bluffs, Virginia, northwest of U.S. Route 301 bridge (type locality for *Osteopygis roundsi*).
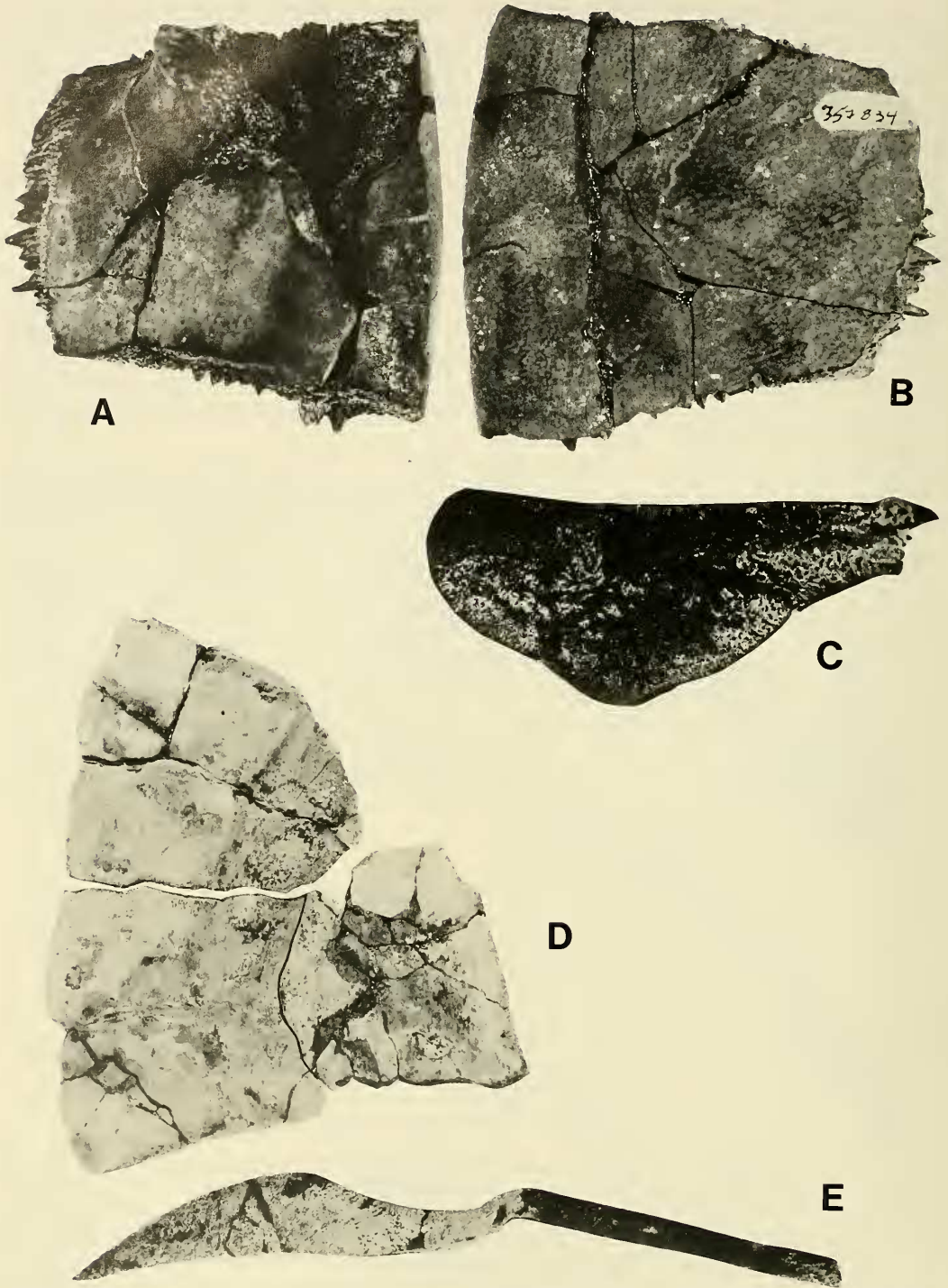
Fig. 3.   Specimens of *Agomphus* and *Taphrosphys* from the Brightseat Formation of Maryland. A, Ventral, B, Dorsal, and C, Anterior view of the third right peripheral element of *Agomphus* sp. Maximum dimension of

pygal, pygal, and eleventh left peripheral elements.

Locality and horizon.—Found in the Brightseat Formation at the Hampton Mall (near the junction of Central Avenue and Interstate 95) in Prince Georges County, Maryland, by Albert Myrick.

Discussion.—This side-necked turtle is a fairly common faunal component of the Hornerstown Sand in New Jersey. A number of nominal species have been described, but these have been reduced to the single taxon *Taphrosphys sulcatus* by Gaffney (1975a), who concluded that the various type materials represent individual variants within a single population. The Maryland specimen shows no significant differences from the New Jersey material and is therefore included in the same taxon.

Family Adocidae
Agomphus sp.
Fig. 3A–C

Referred specimen.—USNM 357834, a third right peripheral element.

Locality and horizon.—Probably found in the Brightseat Formation at the Hampton Mall in Prince Georges County, Maryland.

Discussion.—The great thickness of this element, its incorporation into a massive plastral bridge, the lack of well developed surface sculpturing, and the presence of a very thin sulcal groove all characterize this specimen as an element of *Agomphus*. Although *Agomphus tardus* and *Agomphus masculinus* (Wieland 1905) are based on fairly complete material, the types of *A. firmus, A. petrosus, A. turgidus, A. oxysternum,* and *A. pectoralis* are based on very fragmentary specimens. It is unclear if more than one variable taxon is represented. In the absence of adequate material to resolve

this issue, the specimen from Maryland is merely designated as *Agomphus* sp. The original donor card, which indicates no collector, stated that the specimen came from the Aquia Formation at Hampton Mall rather than the Brightseat Formation. However, examination of the matrix clinging to the specimen shows that it contains muscovite flakes but lacks glauconite or phosphate grains. Because the Brightseat is micaceous but not glauconitic at this locality, while the Aquia is glauconitic but not micaceous, the specimen almost certainly came from the Brightseat rather than the Aquia (Lauck W. Ward, pers. obs. 1987). *Agomphus* is found frequently in the Hornerstown Sand of New Jersey, which is age equivalent to the Brightseat, but is unknown from any other Aquia Formation locality. Therefore, this specimen can be assigned to the Brightseat, rather than the Aquia, with considerable confidence.

Family Cheloniidae
Subfamily Osteopyginae
Osteopygis emarginatus Cope
Figs. 3D, E, 4

Referred specimen.—USNM 412113, palate composed of premaxillaries, maxillaries, and vomer.

Locality and horizon.—Found in the Brightseat Formation at the Hampton Mall in Prince Georges County, Maryland, by George Fonger.

Discussion.—This specimen (Fig. 4, Fig. 11A–C) consists of the major part of a secondary palate. The angle of the beak indicates a broad, blunt snout. These characteristics are typical for *Osteopygis emarginatus*. Although the secondary palate is well developed, it is not so long as in the other known osteopygine genera (*Rhetechel-*

←

specimen is 8.9 cm. D, Ventral and E, Left lateral view of carapace fragment of *Taphrosphys sulcatus*. Ventral view includes pygal (lower left), suprapygal (lower right), and eleventh peripheral (top) elements. Maximum dimension of specimen is 17.8 cm.
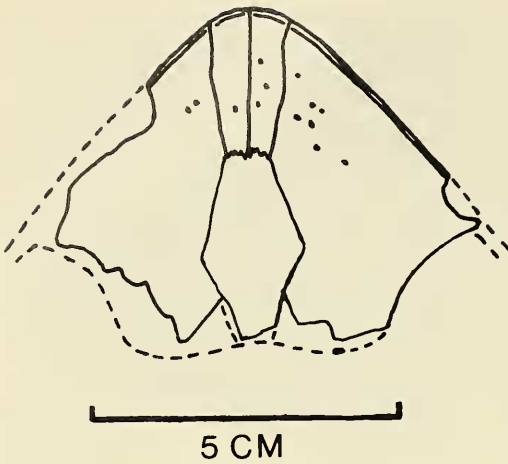
5 CM

Fig. 4. Palate of *Osteopygis emarginatus* Cope based on USNM 412113 from the Brightseat Formation of Maryland.

lys, Erquelinnesia) or in the new species of *Osteopygis* described below. The type material of *O. emarginatus* comes from the Hornerstown Sand of New Jersey, correlative with the Brightseat, so the occurrence of this species in both units is not surprising.

Osteopygis and the Osteopyginae were considered to be toxochelyids by Zangerl (1953, 1971), but Fastovsky (1985) considered their affinities to lie closer to the more advanced family Cheloniidae, on the basis of shared derived cranial characters. This newer taxonomic association is followed here. So far, the Osteopyginae are known only from the Western Hemisphere (Foster 1980, Pritchard 1984).

Turtles from the Aquia Formation

Family Sinemydidae
Planetochelys, new genus

Diagnosis.—Shell small, rounded in dorsal aspect, highly arched and thin. Neural series depressed relative to costals on both sides, producing medial saddle in shell. One suprapygal present. Plastron not sutured to carapace, but a flattened region for abutment of hypoplastral buttresses extending

back to middle of seventh peripheral. Ilia not fused to carapace.

Etymology.—The generic name, from Greek *planetos* (wanderer) and *chelys* (turtle), is an allusion to its apparent familial origins in China.

Planetochelys savoiei, new species
Figs. 5–8

Diagnosis.—Because the genus is currently monotypic, the diagnosis is at present the same as that for the genus.

Etymology.—The species name is for Kurt Savoie, who found the type specimen.

Holotype.—USNM 412107, posterior half of a carapace, found along the western bank of Aquia Creek at the base of Clark & Martin's (1901) "Zone 2" by Kurt Savoie, 1974.

Discussion.—The lack of fusion between the carapace and ilia indicates that this specimen is a cryptodire. The strongly arched carapace lacks a sutured plastral bridge, but does have a flattened area along the ventromedial border of the seventh peripheral (and presumably on the fourth, fifth, and sixth peripherals, which are missing) for abutment of a plastral bridge. Despite its small size and thin bones, there is no sign of any costoperipheral fontanelles. This combination of characters is typical of the Sinemydidae, which were first recognized from Lower Cretaceous beds of eastern Asia (Wiman 1930). Since the description of the type species, *Sinemys lens*, two taxa have been added to this family: *Manchurochelys manchouensis* from the Jurassic of Manchuria (Endo & Shikama 1942) and *S. wierhoensis* from the Cretaceous of Xinjiang, China (Yeh 1973). Recognition at the family level was established by Yeh (1963). Mlynarski (1976) considered the Sinemydidae to be of uncertain affinities, although similarities were noted in the plastron to the plastra of the Dermatemydidae and Kinosterninae. Zangerl (1953) considered the possibility that the Sinemydidae were ancestral to the sea turtles, but he saw no compelling evidence
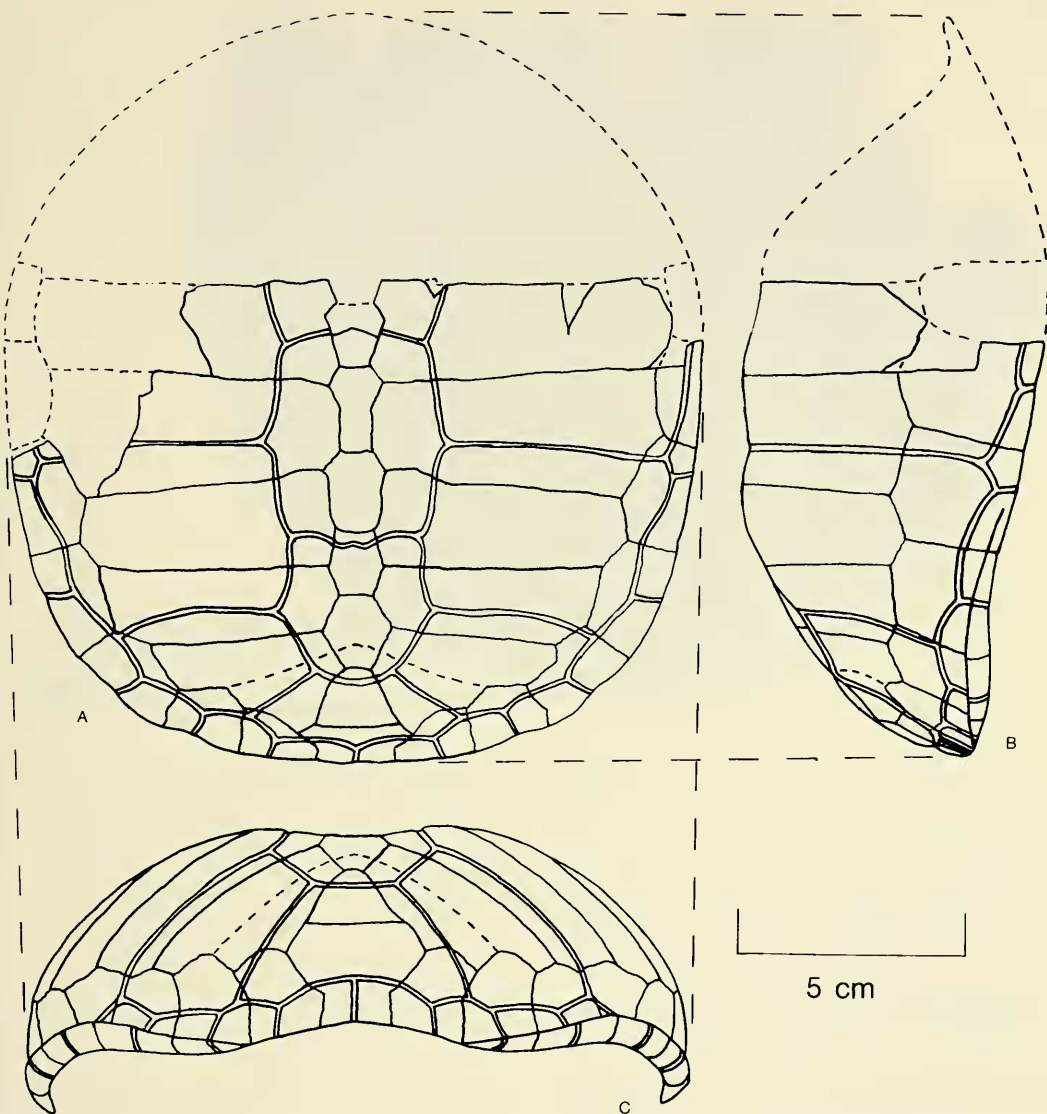
Fig. 5.   A, Dorsal, B, Lateral, and C, Posterior views of the carapace of the type specimen of *Planetochelys savoiei* (new genus and species) (USNM 412107).

for this possibility. Recently, Shuvalov & Chkhikvadze (1979) associated the Early Cretaceous *Hangaiemys* with this family; previously it was considered to be a macrobaenid.

Although the specimen at hand is remote in time and space from other members of the Sinemydidae, its character states are compatible only with this family. Only the Chelydridae and the chelonioid families also lack a sutured plastral bridge, but they have costoperipheral fontanelles when they are as small as this specimen, and they are much flatter in cross section. Even in the late Paleocene, the Chelydridae have their typical strongly crenulated carapace margin (Erick-

Fig. 6.   Dorsal view of the posterior carapace of *Planetochelys savoiei* (USNM 412107).

son 1973), and, by that time, all of the che-
lonioid families were far more specialized
than this form (Zangerl 1953).

The presence of a longitudinal groove
centered along the neural series is reminis-
cent of *Hangaiemys,* and the presence of a
single postneural might be a logical evolu-
tionary result of the trend seen in *Sinemys,*
in which only one large postneural remains
and the other is greatly reduced. Small size
is also a characteristic feature of this group.
In all of these traits, the Aquia specimen
seems to show sinemydid affinities. There-
fore, it is provisionally assigned to that fam-
ily.

Planetochelys differs from *Manchuroche-
lys* in that the latter form still has a partially
sutured plastral bridge and two well devel-
oped postneurals. *Planetochelys* also differs
from *Sinemys* in having only one postneural
and a median longitudinal saddle. *Han-
gaiemys* has two and sometimes three post-
neurals. Because *Planetochelys* is so remote
in time and space from these other forms,

it will probably prove to have many other
unique features when better material be-
comes available. Known portions are shown
in Figs. 5 through 8.

Family Trionychidae
Subfamily Trionychinae
Aspideretes virginianus (Clark), 1895
Figs. 9, 10

Holotype.—USNM 9354, fragments of
two costal plates.

Locality and horizon.—Found at Aquia
Creek bluffs, Stafford County, Virginia. Ho-
rizon unreported but almost certainly Pis-
cataway Member, Aquia Formation, judg-
ing from Clark & Martin (1901:75).

Referred specimen.—USNM 11944,
largely complete carapace except for the dis-
tal portions of the fourth through seventh
costals on the left side.

Locality and horizon.—Found at Aquia
Creek bluffs, Stafford County, Virginia, Pis-
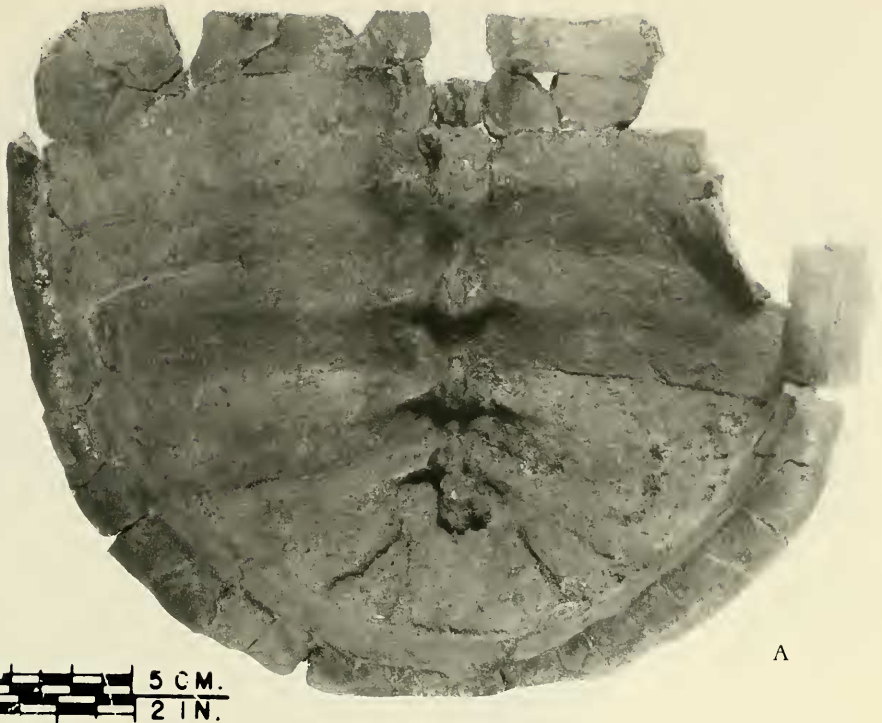cataway Member, Aquia Formation.

Fig. 7.   Ventral view of the posterior carapace of *Planetochelys savoiei* (USNM 412107).

Discussion.—This species is assigned to the subfamily Trionychinae because it lacks peripheral elements, possesses a nuchal that is about five times wider than it is long, and it has a type III disc (Meylan 1984). Hay (1908) accepted the traditional assignment of this species to *Trionyx* (*Amyda*) with a query because the type is so fragmentary. Since Lynn's (1929) description of a fairly complete carapace of *A. virginianus,* no significant new material has been collected. Fragments of this species, common throughout the Piscataway, are easily recognizable by their great thickness and vermiform to pitted sculpture. Only a photograph of Lynn's specimen was published in his paper, and no attempt was made to define the individual shell elements. Much of the periphery of the shell was pieced together, but the central portion of the carapace does not appear to have been reconstructed accurately. By doggedly piecing together the fragments of the central region of Lynn's specimen, I have managed to determine the location of the costal and neural sutures.

As Figs. 9 and 10 show, a large preneural element is present. This element, which may be really the first neural (Meylan 1984), is characteristic of *Aspideretes* but not of *Trionyx.* For this reason, Clark's species is transferred to *Aspideretes.* Probably *Trionyx* proper does not occur in beds older than Eocene (Carpenter 1981). As Hummel (1929:390) has shown, even modern *Trionyx* occasionally can develop a large preneural element. Similarly, the rest of the carapace in modern *Trionyx* can also show a lot of individual variation. Yet preneurals seem to be very exceptional in Eocene to Recent *Trionyx,* whereas they are the rule for Cretaceous to Paleocene *Asperidetes* (Carpenter 1981). A population of shells should be examined to determine accurately

Fig. 8. Oblique (postero-dorsal) view of the posterior carapace of *Planetochelys savoiei* (USNM 412107).

which generic designation is correct, but this is not yet possible. For now, the Paleocene age of this form, the very large size of the preneural in the one nearly complete carapace available, and the absence of evidence for unusual shell development elsewhere in the anterior carapace region serve to characterize this species as a member of *Aspideretes.*

Trionychoids are thought of as exclusively freshwater turtles but have been observed alive in marine waters (Hay 1908:514). The abundance of *Aspideretes virginianus* in the marine Aquia Formation suggests that this form was an inhabitant of marine waters in the late Paleocene (Thanetian). Additionally, the exceptional size, thickness, and massiveness of the carapace and plastron

are compatible with life in sea water, which is more buoyant than fresh water.

Family Cheloniidae
Subfamily Osteopyginae
Osteopygis roundsi, new species
Figs. 12A, 13, 14A, 15

Diagnosis. — Anterior portion of beak blunt and wide; internal edges of maxillary beak project toward anterior midline at an angle of nearly 90°; roof of mouth has an extensive secondary palate. Width to length ratio of vomer 0.68; vomer having prominent medial keel. Back edge of palate formed by contribution from pterygoids. Carapace and plastron, so far as known, typically osteopygine, costoperipheral fonta-
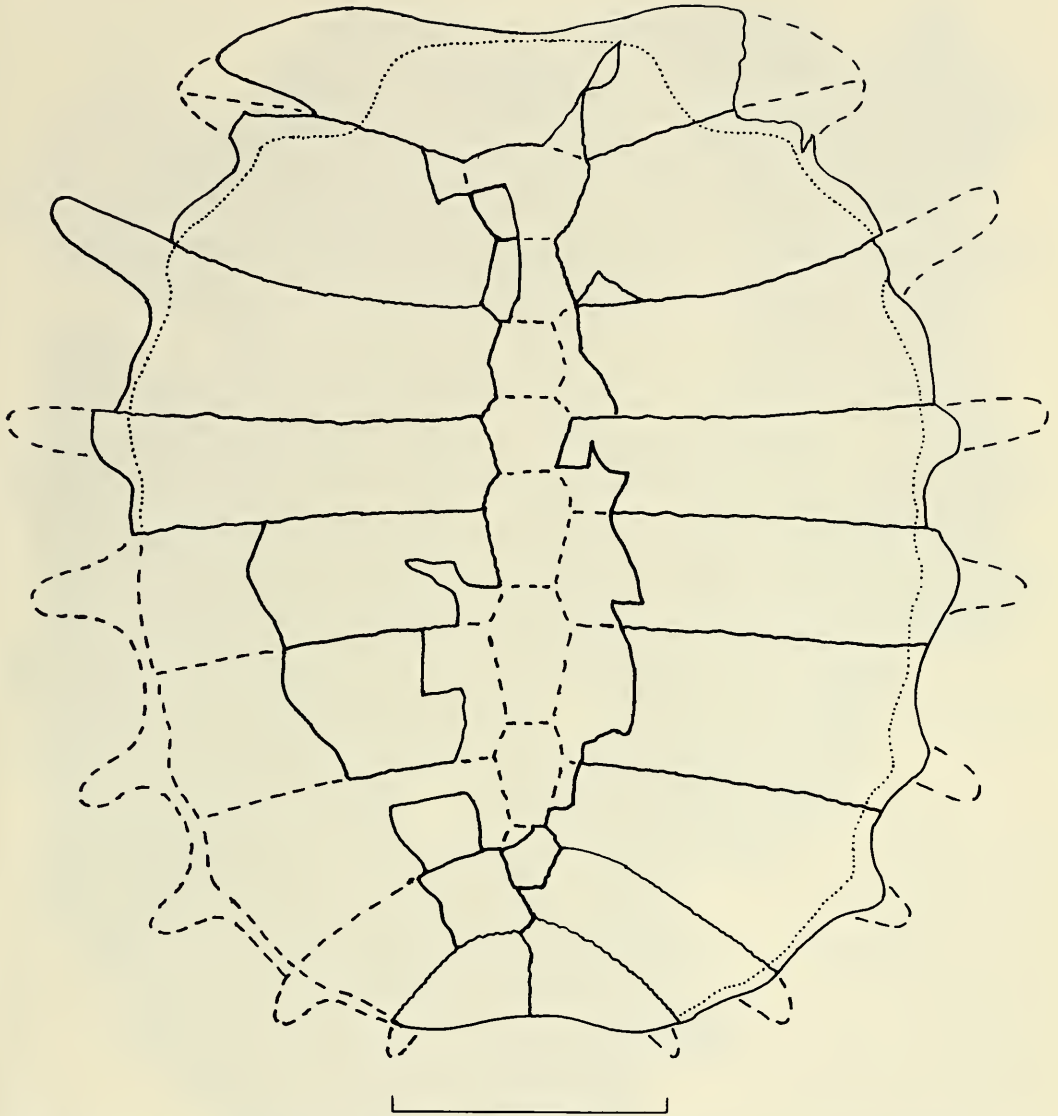
Fig. 9.   Reconstruction of the carapace elements of *Aspideretes virginianus* (Clark) based on USNM 11944.

nelles possibly more persistent than those in *O. emarginatus.* Carapace not sculptured, sulci deeply impressed, costal rib heads sub-rounded in shape.

Etymology.—For Thomas Rounds, who discovered the type specimen.

Holotype.—USNM 412108; a crushed and slightly exploded skull, imbedded in a nodule. Only the ventral surface is clearly visible (Fig. 12A).

Locality and horizon.—Pamunkey River bluffs, upriver from U.S. Highway 301, in the Ashland 7.5-minute quadrangle. Found in shell bed about 1 ft above basal boulder bed, Piscataway Member, Aquia Formation, by Thomas Rounds.

Paratypes.—USNM 357713, poorly preserved skull and associated carapace fragments, including costal fragments, one neural, and three peripherals. River bluff
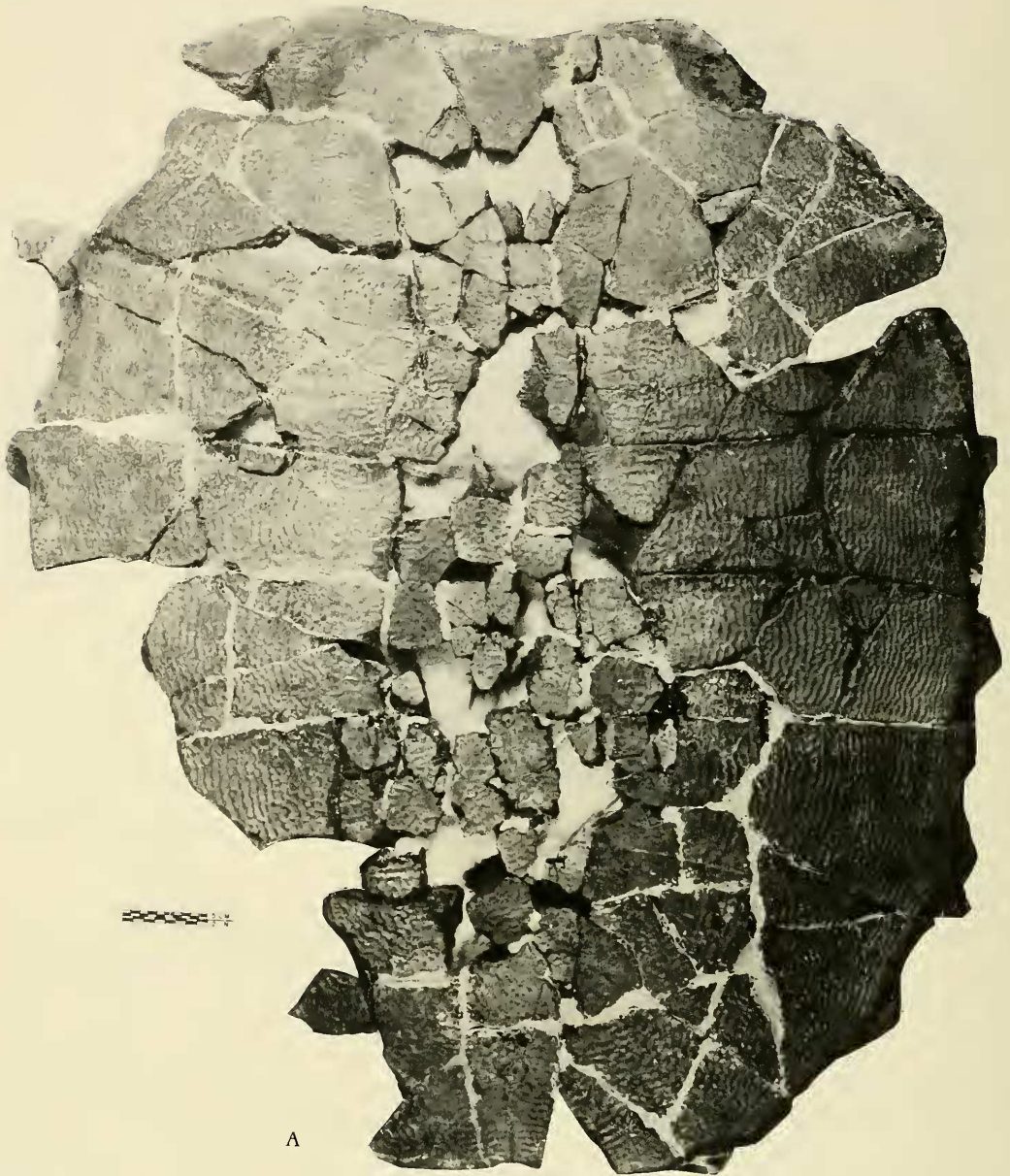
Fig. 10.   Carapace of *Aspideretes virginianus* (USNM 11944).

0.5 mi. south of where the North Anna and South Anna rivers converge to form the Pamunkey River, Ashland 7.5-minute quadrangle. Found in shell bed 2 ft above basal boulder bed, Piscataway Member, Aquia Formation, by Robert E. Weems, Carrol Chewning, Mary Jane Chewning, 1971.— USNM 357710, left hyoplastron and left hypoplastron. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in shell bed comprising "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Calvin Allison.

Fig. 11.   Anterior end of skull of *Osteopygis emarginatus* (USNM 412113). A, Dorsal, B, Lateral, and C, ventral view; length as preserved 5.5 cm; D, Eleventh right peripheral element of *Catapleura ruhoffi,* greatest length 5.5 cm (USNM 358865); E, F, Distal end of tibia of *Dollochelys coatesi* (USNM 412110); G, H, Femur of *Dollochelys coatesi* (USNM 412110).

Discussion.—This species differs from *Osteopygis emarginatus* in being much larger and in possessing a more strongly developed secondary palate. The pterygoids are incorporated into the back of the palate, and the groove receiving the cutting edge of the lower beak is relatively much deeper (Fig. 13). A prominent medial ridge is developed on the vomer; this ridge is developed only faintly in *O. emarginatus.* The general shape of the skull is *Osteopygis*-like and unlike that of *Rhetechelys,* which has a more pointed snout. Although the palate is longer than that in *O. emarginatus,* it is less extremely developed than in either *Erquelinnesia* or *Rhetechelys.*

A second specimen of *O. roundsi* (USNM 357713) also includes a very poorly preserved skull. Little detail is preserved, but the size and the shape of the snout leave little doubt that this specimen represents the same species (Fig. 14A). Associated with the

skull were a number of costal fragments, one well preserved neural, and three peripherals. The neural is flat and notably anteroposteriorly elongate (Fig. 15A). One of the peripherals (Fig. 15B) has a broad notch on its internal border above the socket that received the tip of the costal rib. This feature is also typical of the peripherals of *O. emarginatus.* In *O. emarginatus* the costoperipheral fontanelles eventually closed in mature animals. This closure does not seem to have occurred in the later and more highly derived *Erquelinnesia.* Because *O. roundsi* is intermediate in time and specialization, I suspect that costoperipheral fontanelles may be more persistent in *O. roundsi* than they are in *O. emarginatus.* A partial plastron (USNM 357710) found at Liverpool Point seems typically osteopygine in nature and is tentatively referred to *O. roundsi* (Fig. 15C). The hyoplastron has a long ascending process, as it does in *O. emarginatus,* pre-

Fig. 12. A, Ventral view of skull of *Osteopygis roundsi* (USNM 412108); B, Right anterior side of carapace of *Dollochelys coatesi* (USNM 412109).
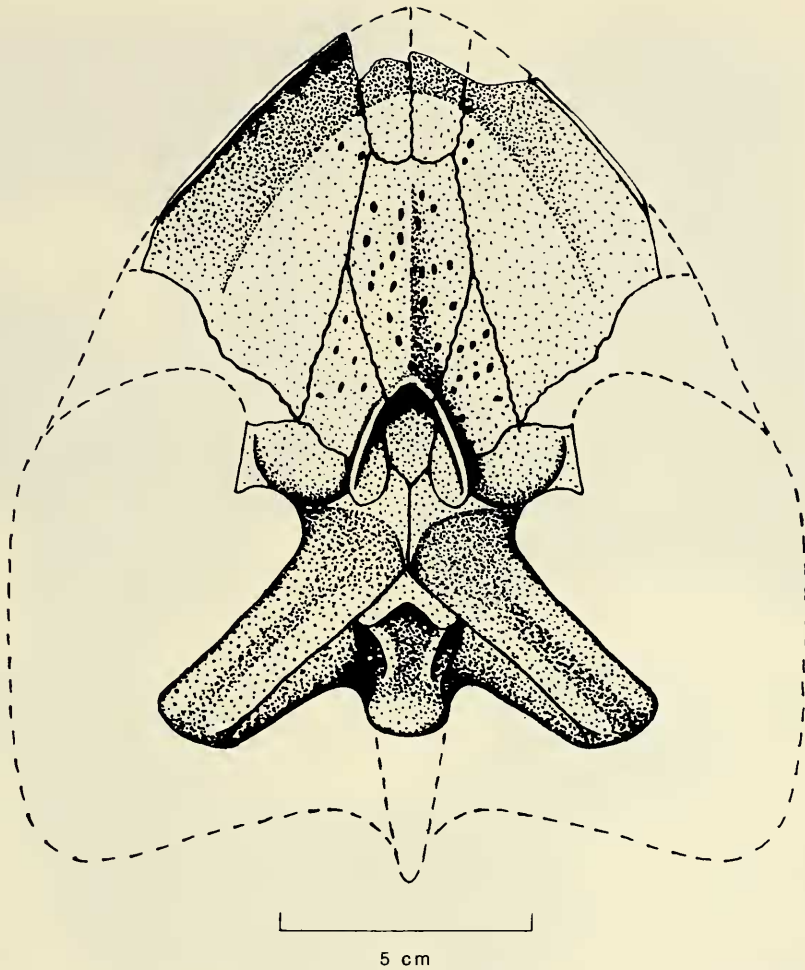
Fig. 13.   Reconstruction of the ventral skull elements of *Osteopygis roundsi* (new species) (USNM 412108).

sumably for insertion into the second peripheral. Another specimen questionably referrable to *O. roundsi* is USNM 9357, which is a costal fragment figured by Clark & Martin (1901:10, fig. 7) as "*Euclastes* sp." It is too large for *Planetochelys* or *Catapleura,* too thick for *Dollochelys* or *Lembonax,* and much too thin and smooth for *Aspideretes.* Therefore, it may be *Osteopygis* by default even though it lacks positive diagnostic characters.

Subfamily Eochelyinae
Catapleura ruhoffi, new species
Figs. 16–19, 20A

Diagnosis. — Dentaries flat and fused along a long, narrow symphysis that includes over two-thirds of length of each element; carapace flattened in lateral aspect, suboval in dorsal aspect. Costoperipheral fontanelles (so far as known) persistent beyond second peripheral. Nuchal much wider than long.
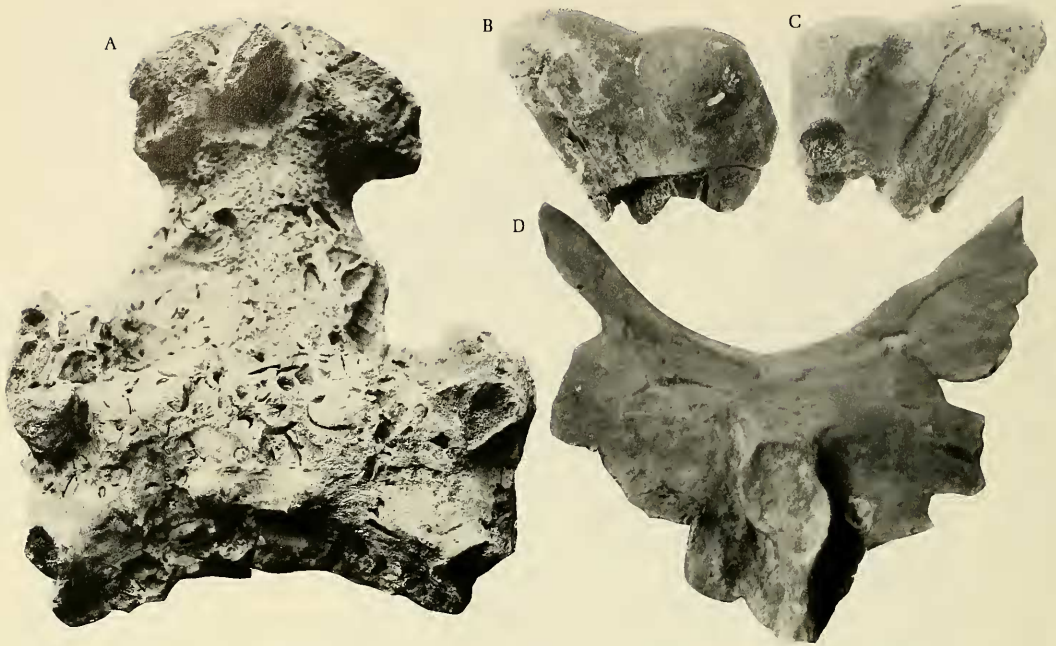
Fig. 14.   A, Poorly preserved skull of *Osteopygis roundsi,* length 19 cm (USNM 357713); B, C, Proximal end of humerus of *Dollochelys coatesi* (USNM 412110); D, Ventral view of nuchal element of *Psephophorus* sp. (from Chandler Bridge Formation (upper Oligocene), Charleston region, South Carolina).

First peripheral much wider along external border than along internal border. Neurals flat anteriorly, slightly keeled posteriorly. Carapace unsculptured, thin boned, sulci lightly impressed onto bone. Costal rib heads subrounded in shape.

Etymology. — For Theodore B. Ruhoff, who discovered the type specimen.

Holotype. — USNM 358865, a disarticulated partial skeleton consisting of the fused dentaries, nuchal, right and left first peripherals, right and left second peripherals, right third peripheral, fifth, sixth and ninth left peripherals, eleventh right peripheral, parts of right and left first costals, part of the right second costal, sixth right costal, first neural, part of fourth neural, eighth neural, and first suprapygal.

Locality and horizon. — West bank of roadcut, Indian Head Road near Piscataway Creek, Prince Georges County, Maryland. Found in Piscataway Member, Aquia For-

mation (in excavation for crocodile) by Theodore B. Ruhoff, 1949.

Discussion. — The fused dentaries of this form (much narrower than one could expect for *Osteopygis roundsi*), a long, narrow symphyseal region, and slightly keeled posterior neurals make this species distinct from all other Piscataway turtles described here (Fig. 16). The fused dentaries are very reminiscent of the Eocene cheloniid *Puppigerus,* and this species may be an ancestral form of that genus. Moody (1974) noted that the length of the dentary symphysis correlated strongly with the length of the secondary palate, and the same correlation probably holds in osteopygines as well. On this basis, the species described here also probably had a secondary palate, a character suggestive of eocheloniine rather than toxochelyine affinities for this form. This species differs from *Puppigerus,* however, in that two fontanelles are present between the first costals and the nu-
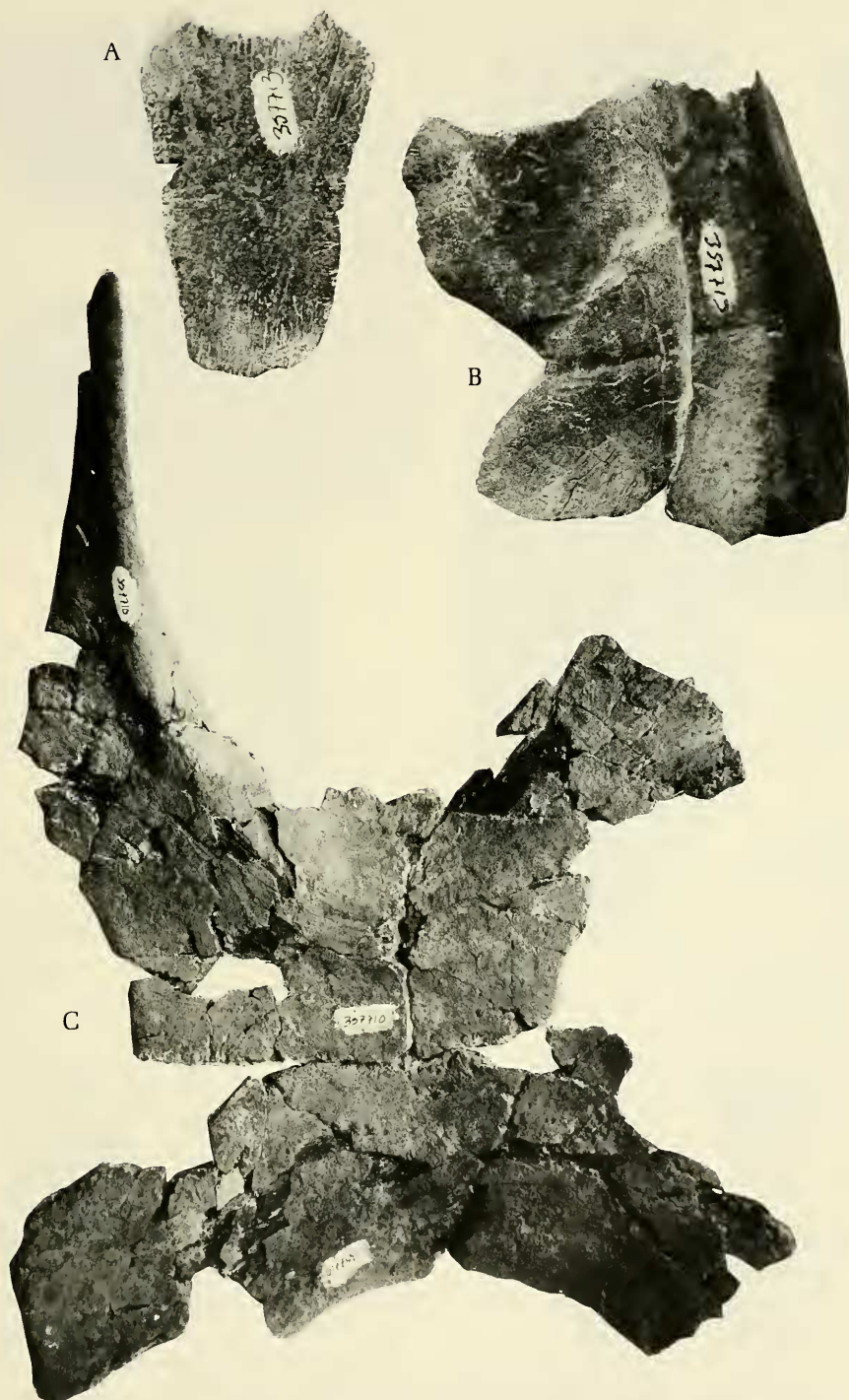
Fig. 15.   Elements of *Osteopygis roundsi*: A, Dorsal view of neural element, length 6 cm (USNM 357713); B, Dorsal view of peripheral element, length 7 cm (USNM 357713); C, Internal view of left hyoplastron and hypoplastron, total length 29 cm (USNM 357710).
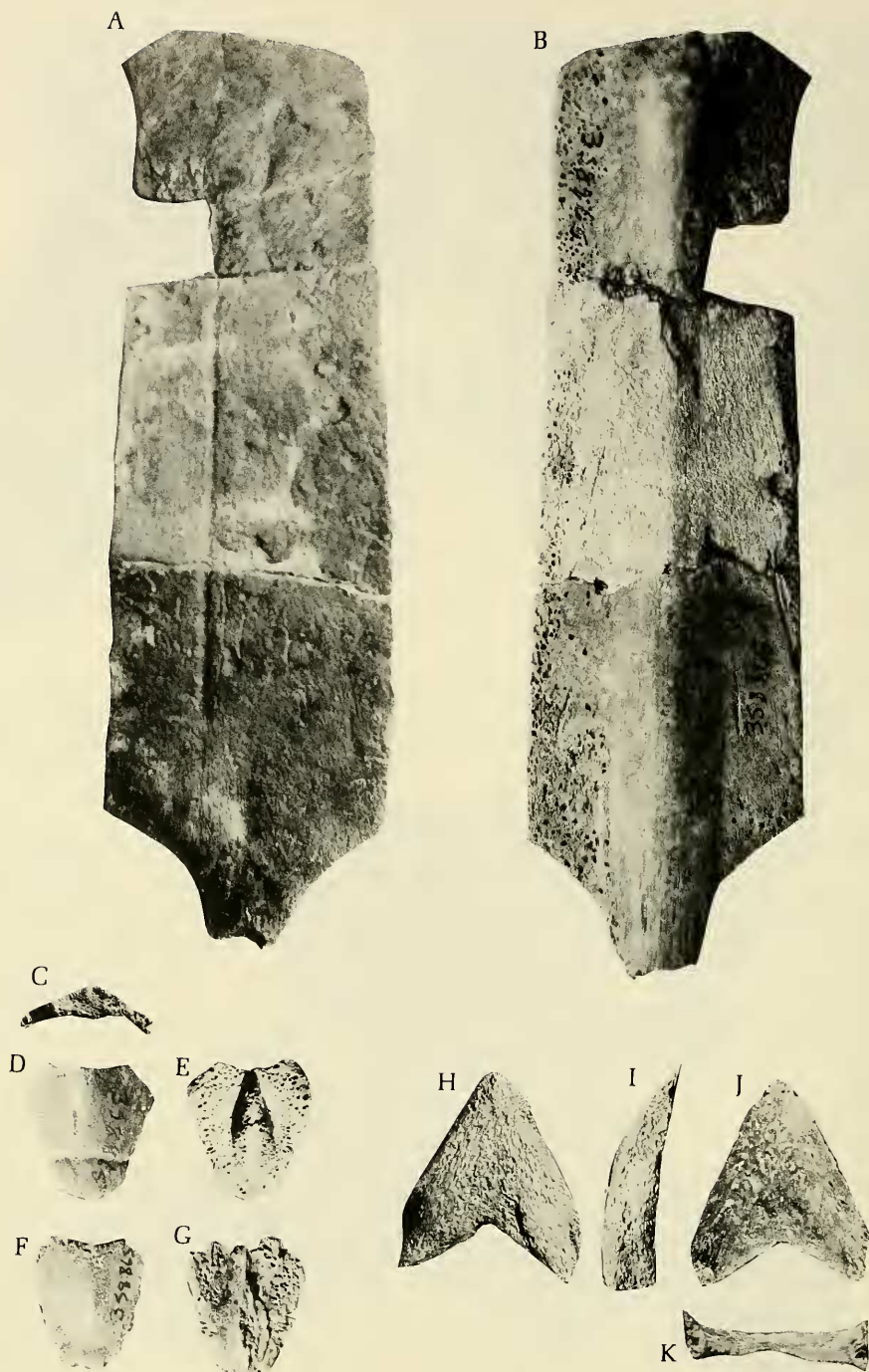
Fig. 16.   Elements of *Catapleura ruhoffi* (USNM 358865): A, B, Sixth right costal in dorsal and ventral view, length as preserved 14 cm; C, D, E, Eighth neural in (C) anterior, (D) dorsal, and (E) ventral view, length 2.3 cm; F, G, First preneural in (F) dorsal and (G) ventral view, length 2.2 cm. H, I, J, K, Fused dentaries in ventral, lateral, dorsal, and posterior view, length 3.4 cm.
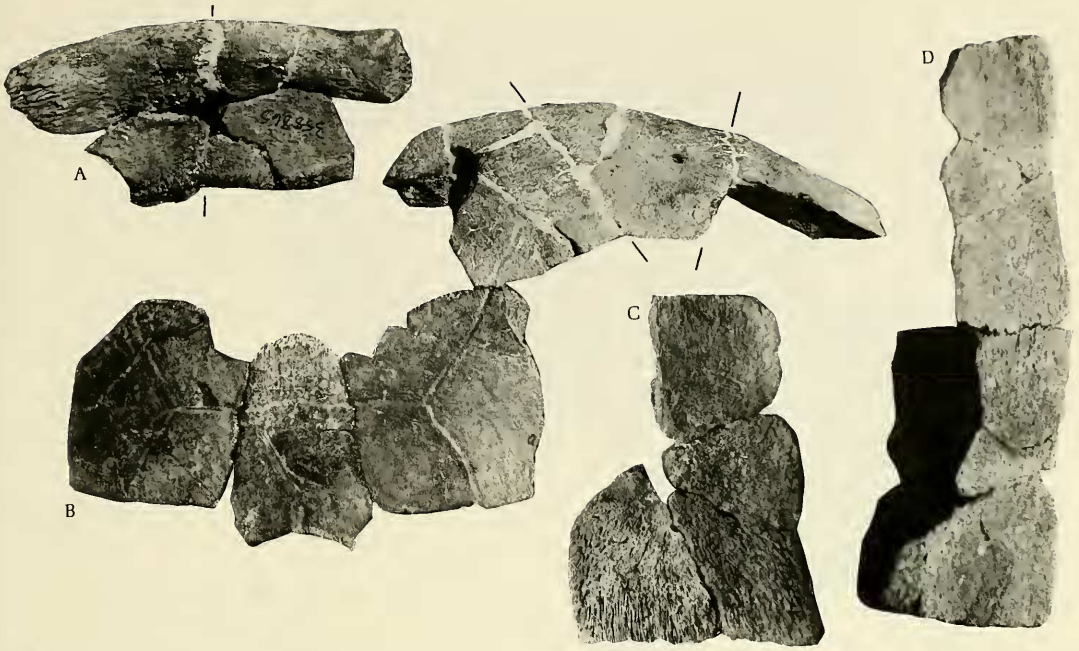
Fig. 17. Elements of *Catapleura ruhoffi* (USNM 358865): A, First and second left peripherals in ventral view, width 8.5 cm; B, First neural, proximal end of first right and left costals, right side of nuchal, first peripheral (edge marked by black lines), and part of second peripheral; neural length 5 cm; C, Ninth left peripheral element, length 7.3 cm; D, Parts of sixth and seventh left peripheral elements, maximum combined length 12.5 cm.

chal in young specimens (Fig. 17) and that the costoperipheral fontanelles apparently are persistent. Probably at an advanced age, the costonuchal fontanelles do become overgrown by a thin layer of bone, as an isolated costal from Liverpool Point shows (USNM 357707, Fig. 20A). Juvenile *Puppigerus* do not appear to have these fontanelles at all. Therefore, although this species may be ancestral to *Puppigerus*, it does not seem to be close enough in morphology to be included in that genus.

Catapleura repanda, from the Hornerstown Sand of New Jersey, is more similar to the Aquia specimen than *Puppigerus*. The type of this species is fragmentary but sufficient to match it to any future, more complete specimens from the Hornerstown. Significant characters are the lack of sculpture, the persistent presence of costoperipheral fontanelles behind the second peripheral, the wide nuchal, and the nearly triangular shape

of the first peripherals. In all of these traits except the last, the new species described here is similar to *C. repanda*. Even in the last character, *C. ruhoffi* approaches *C. repanda*, for the internal margin of the first peripheral is only about one-third to two-thirds as long as the external margin (see Figs. 17 through 19). *Catapleura repanda* is a poorly known type, but its geographic proximity to the new species, despite its temporal distance from it, makes it a genus to which the new form could be assigned. Nothing would be gained at this point by erecting a new genus, because *Catapleura* will probably prove to be the correct generic name when its type species is better known.

Catapleura ruhoffi is placed in the family Cheloniidae because of indirect evidence that this species had a secondary palate (inferred from the long symphyseal region that is present on the fused dentaries) and because of its morphological similarities with
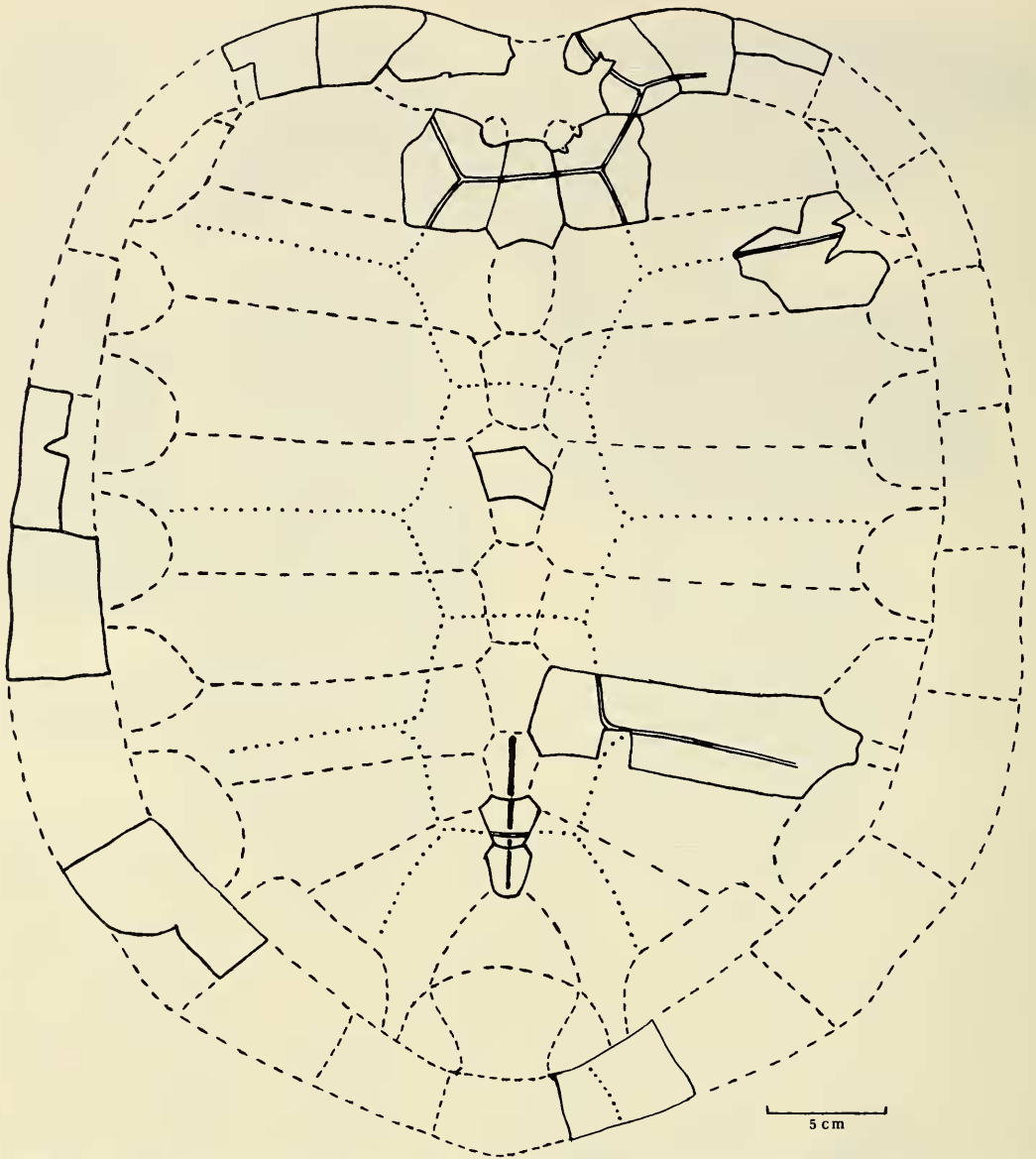
Fig. 18.   Reconstruction of the carapace elements of *Catapleura ruhoffi* (new species) based on the type (USNM 358865).

Puppigerus, which is accepted as a primitive cheloniid. Since the Cheloniidae are derived ultimately from generalized toxochelyid stock, early members of this family should be expected to retain some primitive toxochelyid traits. *Catapleura ruhoffi* is no exception, because it has toxochelyid-like costonuchal fontanelles that became overgrown by bone as the animal matured. The presence of costonuchal fontanelles suggests the possibility that *C. ruhoffi* might be retained within the Toxochelyidae. But *C. ruhoffi* lacks epineural elements or serrations along the external margins of the peripherals, so placement of this species in the Lophochelyinae is precluded. Therefore, *C. ruhoffi*
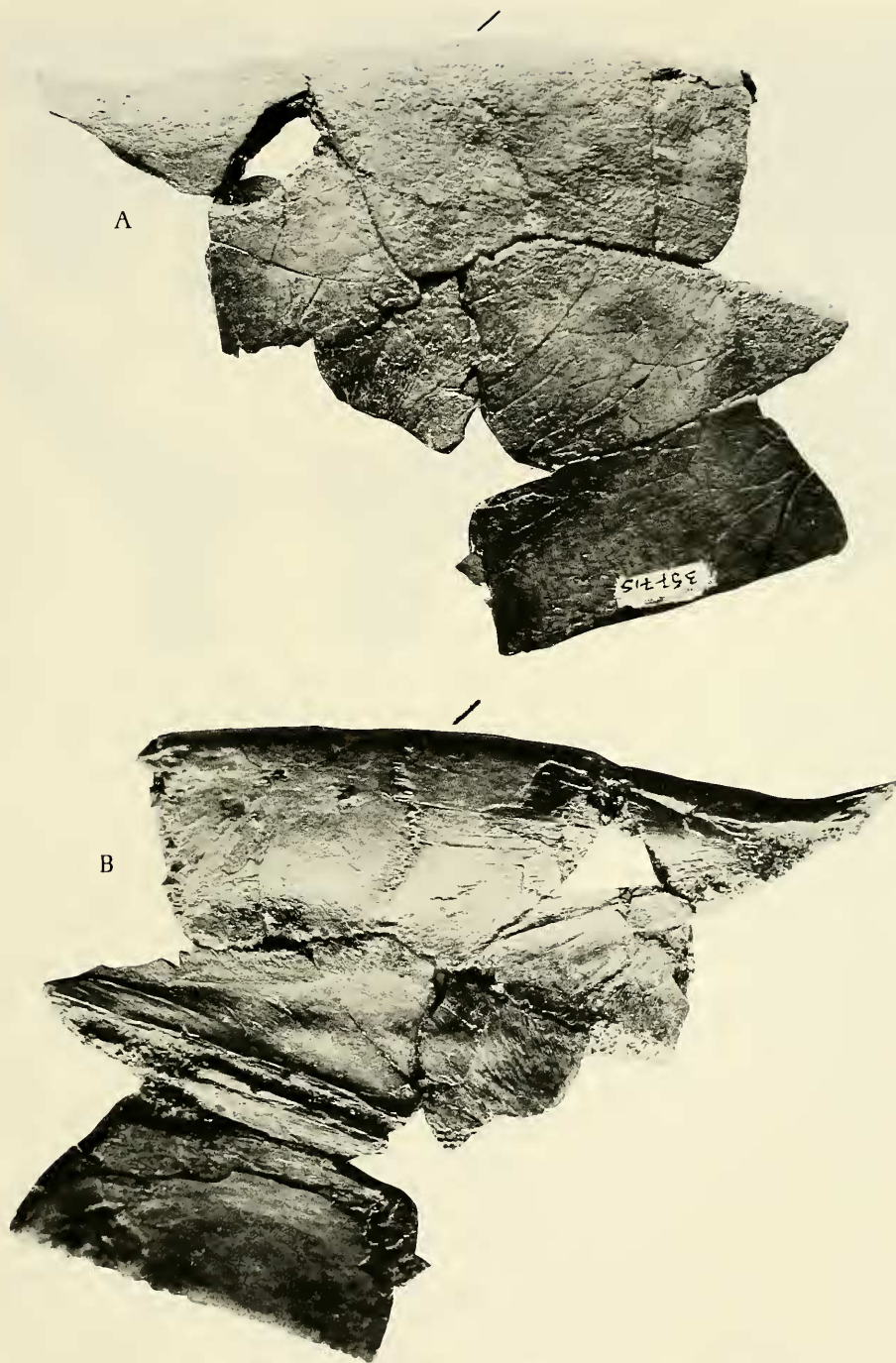
Fig. 19.   First peripheral, part of nuchal, and part of first costal of *Catapleura ruhoffi* (USNM 357715): A, Dorsal view; B, Ventral view. Dark lines mark nuchal/first peripheral suture. Maximum width 15 cm.
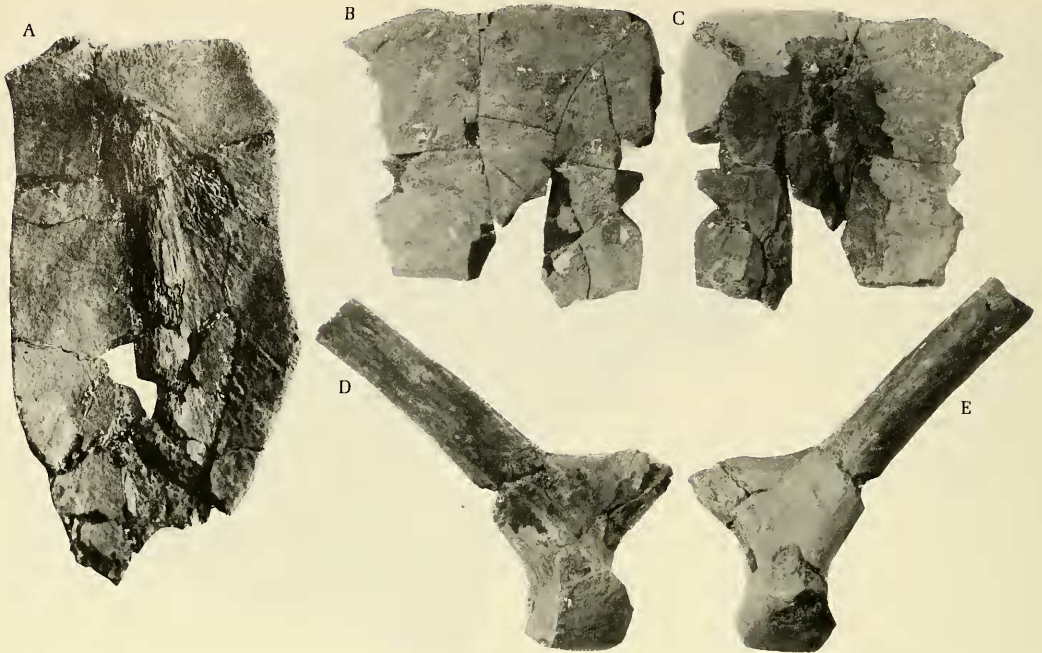
Fig. 20.   A, Internal view of first left costal of *Catapleura ruhoffi* (USNM 357707) showing area of thin bone (upper right corner) where costonuchal fontanelle was present but later thinly overgrown by bone, length 11.8 cm; B, C, Proximal end of second right costal of *Dollochelys coatesi* (USNM 412110) in dorsal and ventral view; D, E, Scapula of *Dollochelys coatesi* (USNM 412110).

could be retained only within the persistently conservative subfamily Toxochelyinae, where it does not fit well because it probably had a long, typically cheloniid secondary palate. Among the Cheloniidae, *C. ruhoffi* cannot be considered an osteopygine, because it lacks a pit for reception of an anteriorly directed spur from the hyoplastron, it has no notches along the internal margin of the peripherals, and the long, narrow shape of the snout is atypical of the Osteopyginae. Therefore, it seems best to view *Catapleura arkansaw* of the Late Cretaceous, *Catapleura repanda* of the early Paleocene, and *Catapleura ruhoffi* of the late Paleocene as representing the primitive cheloniid stock that evolved from generalized toxochelyid ancestors into the modern cheloniid stock. In taxonomic terms, these turtles could be retained as part of the overall Late Cretaceous toxochelyid radiation, but, in evolutionary terms, they already were becoming primitive cheloniids. Therefore, they should be grouped with the stock toward which they were evolving and not with the stock from which they were derived.

Family Toxochelyidae
Subfamily Toxochelyinae
Dollochelys coatesi, new species
Figs. 20B–E, 21, 22

Diagnosis. — First neural scute (and presumably more posterior missing neural scutes by analogy) longer than wide, in contrast with *D. casieri* (type species) and *D. atlantica* which both have neural scutes wider than long; anterior neural elements also proportionally narrower than in the other two species.

Etymology. — For Anthony G. Coates of The George Washington University, my former Ph.D. adviser, who has long worked on the Aquia Formation.
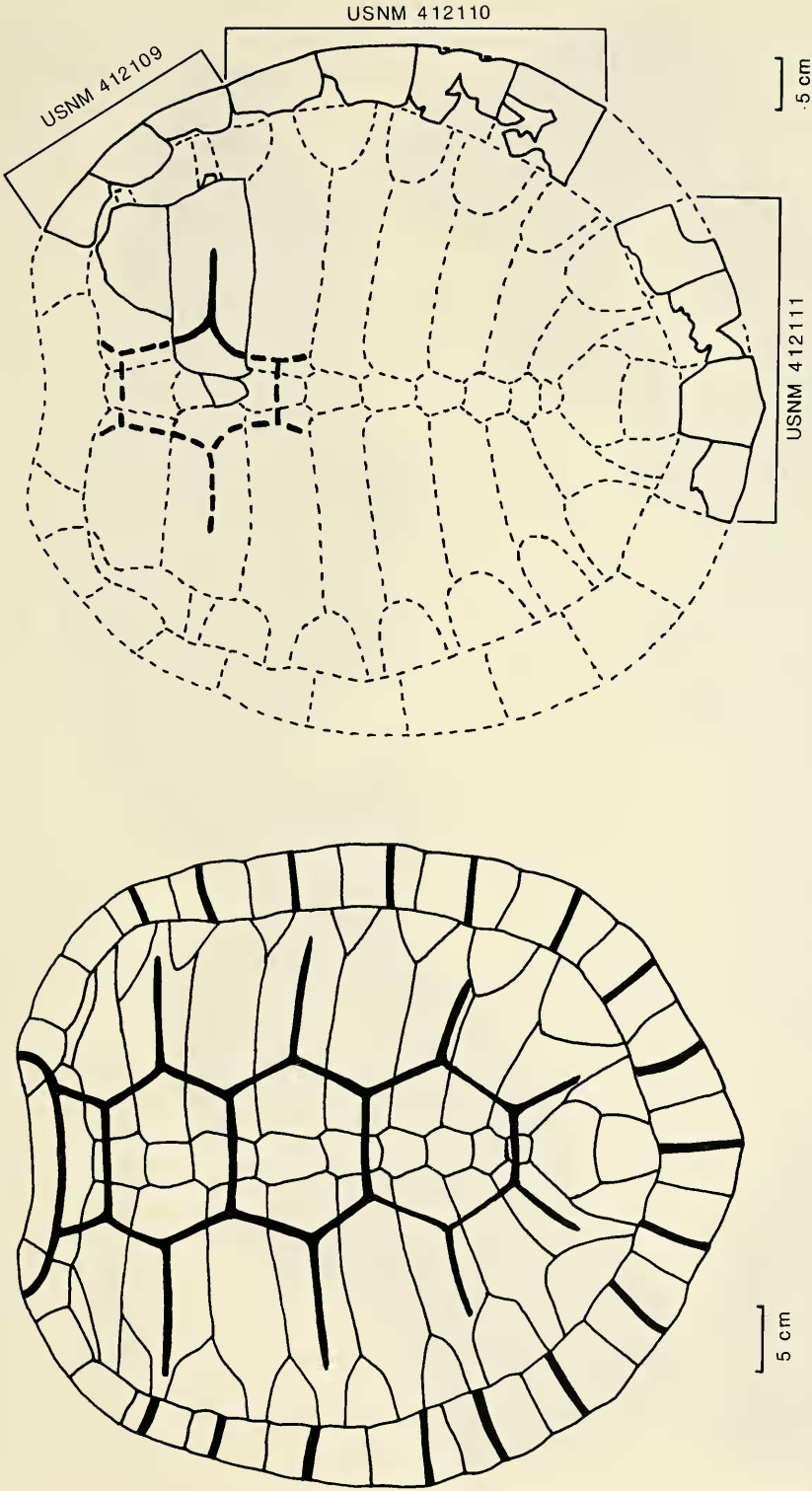
Fig. 21.   Tentative restoration of the carapace of *Dollochelys coatesi* based on USNM 412109, USNM 412110, and USNM 412111 (left side). USNM 412110 also includes the proximal end of the second right costal and some limb and girdle elements (Figs. 11, 14, and 20). Restoration of *D. atlantica* (From Parris and DeTample 1986) is shown for comparison. Note the marked differences in the proportions of the neural elements and the outlines of the first neural scutes.

Fig. 22. Elements of *Dollochelys coatesi*: A, Fifth, sixth, seventh, and eighth peripherals (USNM 412110); B, Tenth right peripheral, eleventh right peripheral, pygal, and eleventh left peripherals in ventral view (USNM 412111).

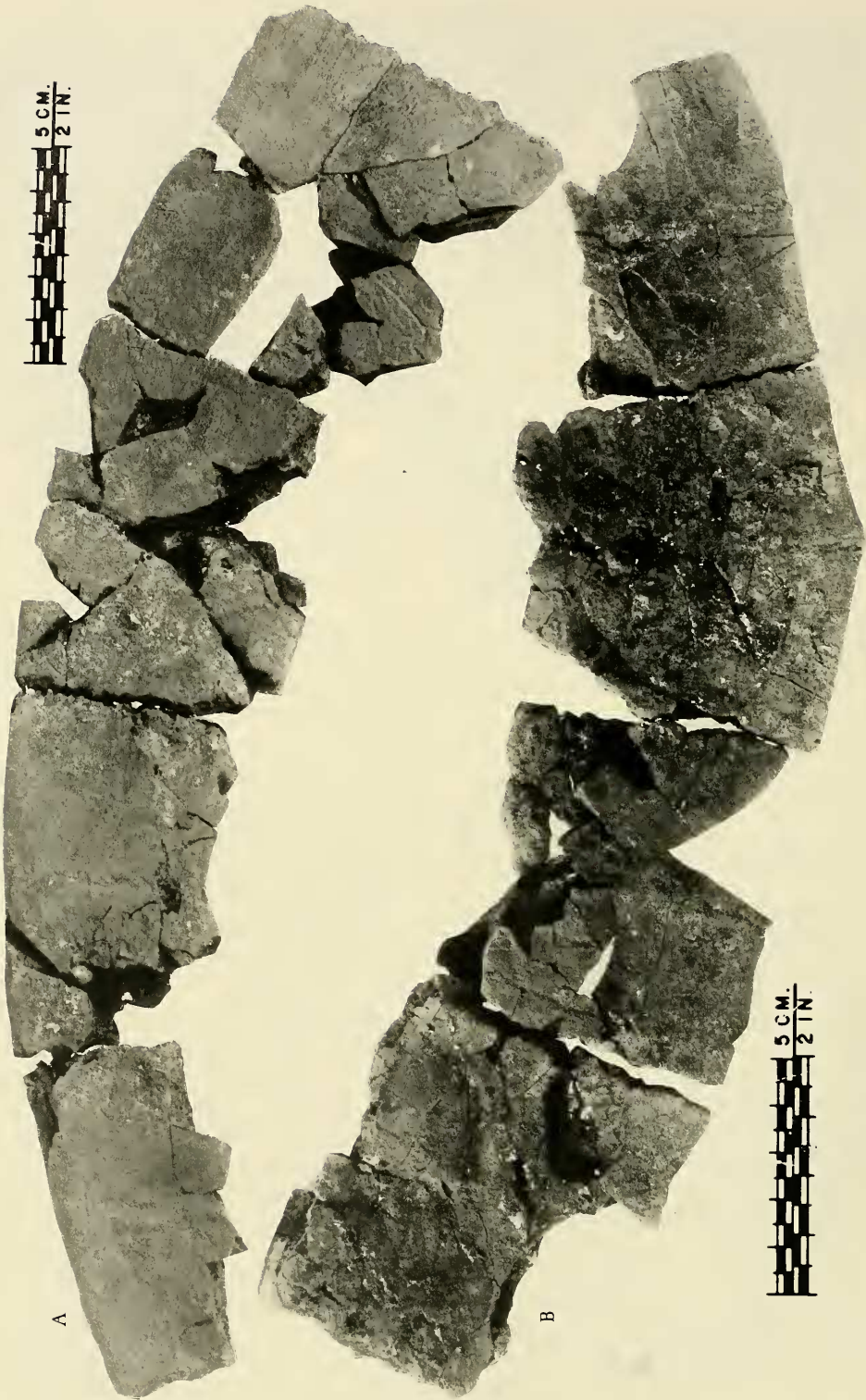*Holotype.* — USNM 412109, part of right first costal, second costal, part of second neural, second through fourth right peripheral. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Robert E. Weems and Stephen R. Horman, 1983.

Paratypes. — USNM 412110, second right costal fragment, pygal fragment, fifth through eighth right peripherals; fragments of the hyoplastra, hypoplastra, and xiphiplastra; scapula, proximal end of right humerus, left femur, distal end of tibia. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Robert E. Weems, Marguerite Kingston, and Terri Purdy, 1977. — USNM 412111, pygal, right and left eleventh peripherals, right tenth peripheral. Bluff south of Liverpool Point, eastern bank of Potomac River, Charles County, Maryland. Found in "Zone 2" of Clark & Martin (1901), Piscataway Member, Aquia Formation, by Stephen R. Horman and Robert E. Weems, May 1983.

Discussion. — The notably thin (2–4 mm thick) costal and neural material of this taxon is typically toxochelyid and cannot be assigned to either of the two thicker-shelled cheloniid turtles previously described in this paper. All three specimens appear to represent a turtle much larger than the new species of *Catapleura* described previously, and the forward extent of the costoperipheral fontanelle (Fig. 21) also is much greater than in *Catapleura* (Fig. 18) even though *Catapleura* represents a much smaller form. The fontanelles in sea turtles tend to close up partly or entirely with age. Therefore, if this material represented an old individual of the same species shown in Fig. 18, the fontanelles should be relatively much more closed. Although the overall carapace size

is comparable to that of *Osteopygis roundsi,* the costal and neural elements are only about half as thick in specimens of comparable size and the peripherals lack the distinctive osteopygine notches on their internal borders (see Fig. 15B).

Among toxochelyids, this material can be assigned only to *Dollochelys* on the basis of USNM 412111 (Fig. 22), which has the characteristic *Dollochelys* pygal shape (as long or longer than wide with a single point at its posterior extremity, see Fig. 21). Other toxochelyid genera all have pygals notably wider than long. The width/length ratio of the pygal in the Piscataway form (0.82) is greater than that for the one well known specimen of *D. casieri* (0.72) but is in the range known for *D. atlantica* (between 0.7 and 1.0). Two other specimens (USNM 412109 and USNM 412110) can be referred confidently to the same taxon on the basis of their relatively large size, very thin shell, lack of notches on the internal border of the peripherals, and extreme development of costoperipheral fontanelles. These specimens are shown on Figs. 12B and 22A and a tentative reconstruction of the carapace, based on all of these specimens, is shown in Fig. 21. The general proportions of the neural and costal elements are similar to those of the same elements in *D. atlantica,* as shown in Fig. 21, though the neurals are somewhat narrower. The most striking difference, however, is shown by the impressions of the sulci which indicate that, in life, the first neural scute (and by analogy probably the other neural scutes as well) was very much narrower than the neural scutes in either *D. casieri* or *D. atlantica.* The carapace fragment shown in Fig. 22A was associated with some limb and girdle elements (Figs. 11E–H, 14B–C, 20B–E) all of which are typically toxochelyid in their morphology. Because limb and girdle elements are poorly known in the other two species, more detailed comparisons of these elements cannot be made.

Fig. 23.   A, Anterior portion of carapace of *Allopleuron insularis* (USNM 359002).

Family Dermochelyidae
Subfamily Allopleurinae
Allopleuron insularis (Cope)
Figs. 23, 24

Referred specimen.—Nuchal, first neural, right and left first peripherals, right and left second peripherals, left third peripheral. Found in bluff between Aquia Creek and Potomac Creek, western bank of Potomac River, Stafford County, Virginia, by Kurt Savoie. Label data do not give exact horizon, but nanofossils in the matrix of the specimen indicate that it came from NP8 (Laurel Bybell, written communication, 1978), which would place it in "Zone 6" of Clark & Martin (1901), Piscataway Member, Aquia Formation.

Discussion.—This fragmentary specimen (Figs. 23 and 24) represents only the anteriormost portion of a very large, lightly built turtle whose carapace was probably over 2 m long. The carapacial bones of this turtle are extremely thin for its size, and the carapace is built very much like a large kite. On the basis of its large size, its deeply indented nuchal, the forwardly projected position of the first peripherals, and its occurrence at only a slightly lower stratigraphic horizon (NP8) than the Vincentown Formation of New Jersey (NP9), this specimen seems identical to *Lembonax insularis* Cope. Unfortunately the type species for *Lembonax, L. polemicus,* is based on only two fragments of plastron and a fragment of scapula, none of which are diagnostic. Therefore, "*Lembonax*" must be considered a nomen dubium, even though the species "*Lembonax*" *insularis* and "*Lembonax*" *propylaeus* Cope are apparently based on diagnosable material and therefore valid. Fortunately, the well known European turtle genus *Allopleuron* Ruschkamp agrees with all of this material in its most striking features, so there is no difficulty in assigning both "*L.*" *insularis* and "*L.*" *propylaeus* to that well known genus.

Cope and later Hay (1908) recognized that the first peripheral in *A. insularis* was located in a very peculiar position. Although Cope correctly recognized that this element was the first peripheral, Hay was uncertain and thus speculated that the same element might be the eleventh peripheral. Reference to the present specimen shows that much of the confusion resulted from the fact that the first peripheral has been ontogenetically drawn forward, so that the second peripheral makes broad contact with the nuchal behind it. This very unusual ontogeny has caused the first peripherals to form the inner edges of two horns that project forward on either side of the neck. Correlatively, the nuchal edges have been drawn forward to give the nuchal a deep, saddle-shaped anterior border similar to that found in *Allopleuron propylaeus* and *A. hoffmani,* both of which are close to this form but differ significantly from the Aquia specimen in the details of the shape of the nuchal. On the basis of the unsutured inner margin of the second and third peripherals, *A. insularis* appears to have had a long, open costoperipheral fontanelle. The first neural is notable for being nearly triangular in shape and much wider than it is long. The costals are unknown. The wide neural is very reminiscent of the condition found in *Eosphargis breineri* (Nielsen, 1964), a primitive dermochelyoid turtle (Rhodin 1985:766), and even the Cretaceous form of *Allopleuron* shows a trend in this direction, its neurals being about as wide as they are long.

Recently, a partial skeleton with a *Psephophorus*-type dermal shield was found in the upper Oligocene Chandler Bridge Formation near Charleston, South Carolina. Associated with this specimen was a thin nuchal plate having a deeply emarginated anterior border (Fig. 14D). On the basis of this association, as well as the similarities of *Allopleuron* with *Eosphargis,* it seems clear that *Allopleuron insularis* is part of the ancestral stock of the modern *Dermochelys.* However, this ancestral stock (*Glyptochelone, Allopleuron, Protosphargis,* and *Eos-*
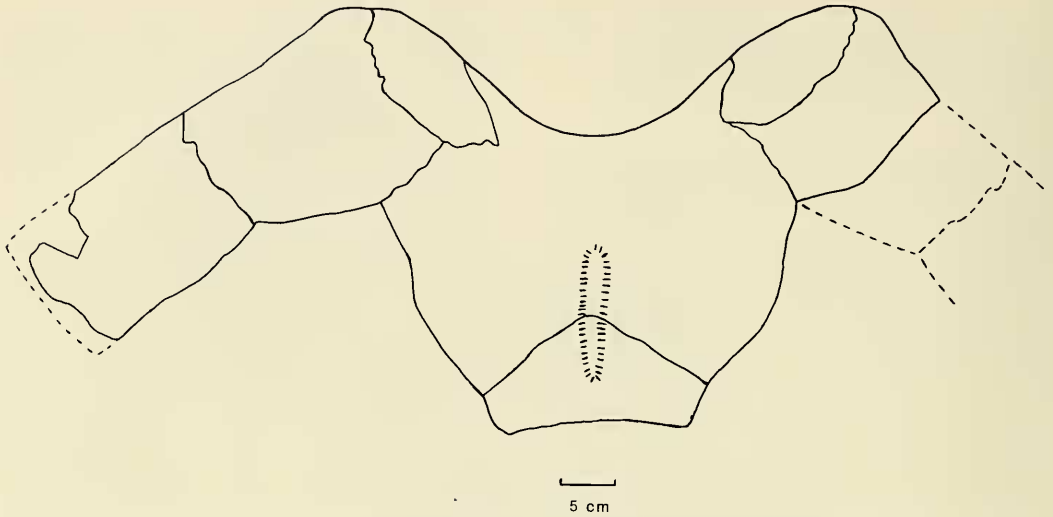
Fig. 24.   Restoration of the anterior part of the carapace of *Allopleuron insularis* (Cope) based on USNM 359002.

phargis) completely lacks the uniquely dermochelyid armor of polygonal mosaic plates and so merits separate subfamilial rank. It is considered best to use the well known genus *Allopleuron* as the namesake for this subfamily. The Allopleurinae can be defined as including large, relatively very thin-shelled, strongly fontanellized sea turtles having strongly reduced, anteroposteriorly elongate plastral elements, a deeply excavated nuchal element, but no development of dermochelyid mosaic armor.

Implications for the Phylogeny of Sea Turtles

The foregoing descriptions suggest that the Paleocene sea turtles of New Jersey, Maryland, and Virginia provide an evolutionary link between the Late Cretaceous sea turtles of the American western interior and the Eocene sea turtles of England and Belgium. Zangerl (1971) suggested that the toxochelyids appeared and persisted later in western Europe than they did in North America, and argued that this phenomenon was the result of their slow dispersion over geologic time from west to east. Recently, however, Moody (1980b) has pointed to recent discoveries of Cretaceous toxochelyids from Ireland and France indicating that the family was widespread throughout the North Atlantic Basin in Late Cretaceous time. Because Eocene sea turtles are very poorly known in both the Atlantic and Gulf Coastal Plains of America, nothing meaningful can be inferred about their American distribution at that time, but there is currently no positive evidence to suggest that sea turtles in Europe or America were strongly endemic. Although exactly equivalent faunal horizons on each continent cannot so far be matched, the presence in the American Paleocene of forms that seem close to the expected ancestral condition for European Eocene forms strongly suggests that migration back and forth across the Atlantic was as easy then as it is for sea turtles today.

Although Zangerl (1953) did not attempt to draw a phylogenetic chart of American Cretaceous sea turtles, such a chart can be produced readily from his taxonomic treatment. The present perspective (and a much more complete knowledge of Paleocene forms) seem to warrant reinterpretation of

the phylogeny of sea turtles as envisioned by Zangerl. This reinterpretation results from changing the taxonomic position of just two closely related genera, *Desmatochelys* and *Corsochelys*. Zangerl considered both to be early cheloniids, largely because of basicranial specializations that also are seen in modern cheloniids. Yet, because parallelism is common in closely related lineages, it is reasonable to expect different lineages of sea turtles to evolve one trait (or a few functionally related traits) in parallel. In some traits, particularly the strong forward projection of their nuchals, *Corsochelys* and *Desmatochelys* are uniquely specialized sea turtles. In other respects, however, recent workers have tended to find greatest similarities with the Dermochelyoidea. Pritchard (1979) associated *Desmatochelys* with the dermochelyoids, and Rhodin (1985) has shown that *Corsochelys* had vascularized chondroepiphyses, a character state otherwise known only among the dermochelyoids. Also, both genera show an early trend toward large size and strong reduction in the carapace. Another notable dermochelyid trait is the fact that both the left and the right rows of plastral elements are drawn strongly away from the midline and compressed side to side to leave a medial fontanelle across the entire central half of the plastral area. This pattern is typical of that found in the Allopleurinae and Dermochelyinae. In contrast, the Protostegidae retain primitive, squarish, plate-like elements (Zangerl 1953, Collins 1970), and the Cretaceous chelonioid families have their plastral elements compressed anteroposteriorly toward the midline to leave large anterolateral and postero-lateral fontanelles but only a narrow median fontanelle (see Fig. 25 for comparisons).

Although the plastral elements appear compressed, the likely ontogenetic mechanism to effect this appearance probably was the establishment of a line or lines of polarity, perpendicular to which growth was retarded. By slowing growth along one axis of plastral elements, intervening cartilaginous areas remained unreplaced. This reduced weight and the need to ingest as much phosphorus to generate more bone. Strength along the axis parallel to the line or lines of polarity, however, was not sacrificed because the narrow but elongate plastral elements still formed bracing struts. Thus a balance was struck between the advantages of lightening the shell and the disadvantages of weakening it.

The fact that the protostegids retain essentially plate-like plastral elements, yet in other respects are readily allied with the dermochelyids rather than with the chelonioids (see Fig. 26), strongly suggests that ontogenetic mechanisms to effect extreme plastral reduction evolved independently in chelonioids and dermochelyids. Similarly, because chelonioid turtles and dermochelyid turtles effect the reduction of their plastrons by contraction of elements along axes with orthogonal polarities, it is difficult to envision an ancestor which could have had character states common to both strategies. The modern genus *Chelonia* is the only sea turtle known to develop both longitudinal and (secondarily in the late Tertiary) lateral compression of its plastron. All other sea turtles seem to follow one pattern of condensation to the exclusion of the other. This strong contrast in developmental style offers two obvious derived character states which can be used to separate chelonioid from dermochelyid turtles.

On the basis of all of the above derived character traits, it is most reasonable to ally *Desmatochelys* and *Corsochelys* with the Dermochelyidae. However, they obviously merit rank as a discrete subfamily, the Desmatochelyinae, because they are readily distinguished within the Dermochelyidae by the presence of forwardly thrust nuchals. With the placement of *Desmatochelys* and *Corsochelys* in the Dermochelyidae, a taxonomy can be erected for sea turtles which also makes sense of their stratigraphic occurrences as well.
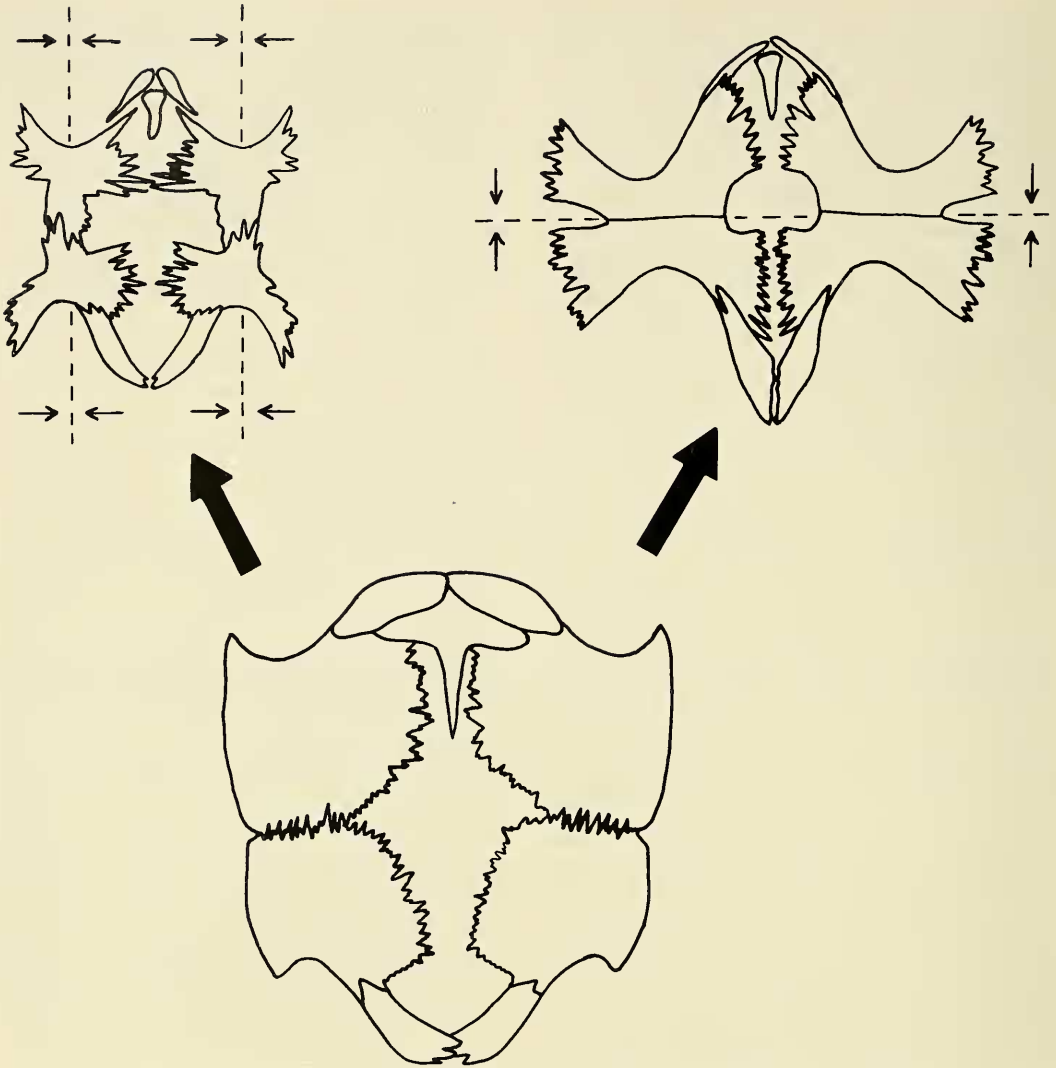
Fig. 25. Diagram showing the two major evolutionary trends in the plastrons of advanced sea turtles. Primitively the plastral elements are squarish and only slightly reduced, as illustrated by the Chelospharginae (bottom). In more advanced dermochelyoid forms, there is a tendency for the plastral elements to become more reduced by compression (shown by arrows) toward two axes (dashed lines) oriented in an anteroposterior direction, leaving a very broad medial plastral fontanelle (upper left). In cheloniid and toxochelyid turtles, the plastral elements tend to become compressed toward a single axis oriented transversely across the midline of the shell (upper right), leaving broad anterolateral and posterolateral plastral fontanelles. In the living *Chelonia mydas,* both types of compression seem to occur, but this is a highly derived condition, established in the Late Tertiary, atypical of other cheloniids.

Because the entire superfamily to which the Dermochelyidae belong is so thin-shelled and fontanellized, well-preserved specimens are rare. It therefore seems likely that many more species of Cretaceous and early Tertiary dermochelyids remain to be described and that any phylogeny of this family made at the present time will be neces-

sarily sketchy and very incomplete. Similarly, the details of the phylogeny of the family Cheloniidae are still sketchy and incomplete due to lack of described material at many horizons. Nevertheless, at the subfamily and higher taxonomic levels, a cladistic phylogeny can be drawn relating all of the various known families and subfamilies of sea turtles on the basis of shared derived characteristics (see Fig. 26). This proposed phylogeny 1) entirely removes occurrences of apparently advanced cheloniids from the Cretaceous and 2) implies that the Dermochelyidae occur as far back in time as unequivocal members of the Toxochelyidae. *Kirgizemys,* which was described by Nessov & Khozatskiy (1978) as a Lower Cretaceous toxochelyid, is extremely primitive and shows only a few derived toxochelyid traits in its shell, such as developing lateral plastral fontanelles and a tendency toward anteroposterior constriction of the plastron toward the midline. The familial assignment is quite possibly correct, but without cranial material it is impossible to be certain based on so few observable derived toxochelyid character states.

Although the Dermochelyidae, as here defined, seem to stand in contrast to the Toxochelyidae and Cheloniidae, they do show some affinities with the Protostegidae, principally in the strongly reduced carapace, the proportions of elements in the shoulder girdle, and the morphology and histology of the humerus. Therefore, it is reasonable to associate these two families within the superfamily Dermochelioidea as an entirely separate line of sea turtle evolution from the Toxochelyidae and Cheloniidae, which can be associated together as the superfamily Chelonioidea. The four constituent families of these two superfamilies are the same four recognized by Gaffney (1975b) as containing all Cretaceous and Cenozoic sea turtles. The taxonomic organization of these various families and subfamilies, and the described genera which can be assigned con-

Table 2.—Taxonomy of the sea turtles, showing superfamily, family, and subfamily levels of classification and their organization. Below the subfamily level, phylogenetic pathways are not indicated and genera are listed *seriatim.*

Superfamily Chelonioidea
  Family Plesiochelyidae
    Plesiochelys, Portlandemys

  Family Toxochelyidae
    Subfamily Toxochelyinae
      Dollochelys, ?Kirgizemys, Portochelys, Thinochelys, Toxochelys
    Subfamily Lophocheliinae
      Ctenochelys, Lophochelys, Neurochelys, Peritresius, Prionochelys

  Family Cheloniidae
    Subfamily Osteopyginae
      Erquelinnesia, Osteopygis, Rhetechelys
    Subfamily Eocheloniinae
      Argillochelys, Catapleura, Eochelone, Glarichelys, Puppigerus, Tasbacka
    Subfamily Syllominae
      ?Bryochelys, Kurobechelys, Syllomus
    Subfamily Cheloniinae
      Caretta, Carolinochelys, Chelonia, Eretmochelys, Lepidochelys, Procolpochelys
Superfamily Dermochelyoidea
  Family Protostegidae
    Subfamily Chelospharginae
      Calcarichelys, Chelosphargis, Rhinochelys
    Subfamily Protostegidae
      Archelon, Protostega

  Family Dermochelyidae
    Subfamily Desmatochelyinae
      Corsochelys, Desmatochelys
    Subfamily Allopleuroninae
      Allopleuron, Eosphargis, Glyptochelone, Protosphargis
    Subfamily Dermochelyinae
      Cosmochelys, Dermochelys, Psephophorus

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fidently to them, are summarized in Table 2.

Once *Desmotochelys* and *Corsochelys* have been removed from the Chelonioidea, the major evolutionary radiation of the Cheloniidae cannot be found before the beginning of the Tertiary. Persistently generalized sea turtles, possibly similar to *Thinochelys* and *Portochelys,* appear to have given rise to a primitive cheloniid, *Catapleura arkansaw,* by the Late Cretaceous
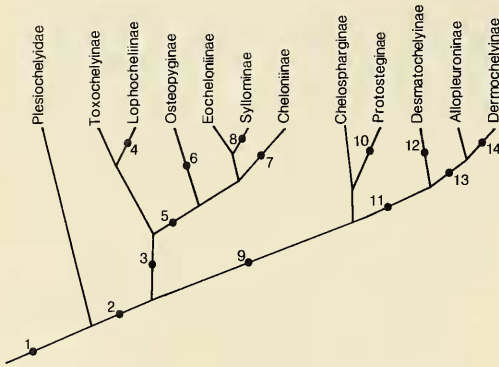
Fig. 26.   Cladogram showing the relationships and key shared derived characters of the known families and subfamilies of sea turtles. Numbers refer to the following character states or character complexes: 1) Palatine and internal carotid arteries equal in diameter, basisphenoidal trabeculae lie close together; foramina anterius canalis carotici interni lie close together and are separated by relatively thin bar of bone; dorsum sellae high and separated from sella turcica and carotid foramina by prominent bone surface; posterior part of sella turcica not concealed by overhanging dorsum sellae (Gaffney 1975b, 1984). 2) Palatine artery and canalis caroticus lateralis larger than internal carotid artery and canalis caroticus internus; front limb with elongate digits and metacarpals forming a flipper with elements oriented in one plane (Gaffney 1975b, 1984). 3) Hyoplastra and hypoplastra reduced by constriction anteroposteriorly toward a transverse midline axis (see Fig. 25). 4) Neurals serrated, forming mid-dorsal keel, peripherals moderately to strongly serrated, connection between pygal and suprapygal very narrow or broken, hyoplastron, hypoplastron, and xiphiplastron with conspicuous ventral keel knobs, epineural elements present in advanced genera (Zangerl 1953). 5) Secondary palate present, postnuchal fontanelles lost at least in adult stages. 6) Prefrontal has an extended posterior process, nearly or entirely excluding frontal from orbit, fissura ethmoidalis deep, palate flat with low tomial ridge, vomer has straight contact with premaxillaries, enlarged complete secondary palate organized differently from that in the Cheloniinae (Fastovsky 1985). 7) Secondary palate completely developed, rear limbs markedly modified for swimming rather than walking. 8) Secondary palate lost, jaw margins develop pseudodont crenulations, deltopectoral crest of humerus moved far distally toward the middle of the humerus. 9) Much of dermal bone layer absent in carapace, resulting in costal ribs that are free of overlying bone; front flippers very long in relation to body; large radial crest of humerus displaced distally, humerus tends to develop vascularized chondroepiphyses; braincase partially cartilaginous in adult (Wieland 1906, Zangerl 1953, Gaffney 1984, Rhodin 1985). 10) Pointed and

(Schmidt 1944). But only later, in the late Paleocene, did the major radiation of cheloniids begin. Late Cretaceous (Santonian through Campanian) radiations of sea turtles did occur, but these only involved the families Toxochelyidae, Protostegidae, and Dermochelyidae. This major radiation ended with the Campanian, however, and no protostegids of any kind are known to have survived into the Maastrichtian. The toxochelyines are known only from a single form in the Maastrichtian (*Toxochelys weeksi*), and *Dollochelys* is the only known Paleocene form. Similarly, the lophochelyines are represented only by *Peritresius* in the Maastrichtian and a single fragmentary form from the Danian (Wood 1973). In contrast, a modest radiation of the Allopleurines occurred in the Maastrichtian and the osteopygines make their first appearance. In general, though, both the Maastrichtian and Danian appear to have been times of relatively low sea turtle diversity. This general pattern of decline reverses in the Thanetian with the beginning of the cheloniid radiation. In the Ypresian (early Eocene), sea turtles reached their peak of Cenozoic diversity. Although lophochelyines make their last appearance in the form of *Neurochelys* (Moody 1980a), and osteopygines in the form of *Erquelinnesia* (Zangerl 1971), most of this assemblage consists of eochelyines and allopleurines. The later Tertiary history of the sea turtles so far is too poorly known to indicate exact relationships or to get a feeling for detailed changes in diversity.

←

decurved beak; nasal elements lost; costals very greatly reduced, extending no farther down the axis of the rib than a distance equal to their width (Zangerl 1953). 11) Hyoplastra and hypoplastra reduced by constriction laterally toward two parallel anteroposterior axes (see Fig. 25). 12) Nuchal elongated to project forward over neck region, neurals longer than wide. 13) Nuchal element deeply emarginated, neurals as wide or wider than long. 14) Normal shell elements (reduced) overlain by mosaic of suturally interconnected dermal bones.
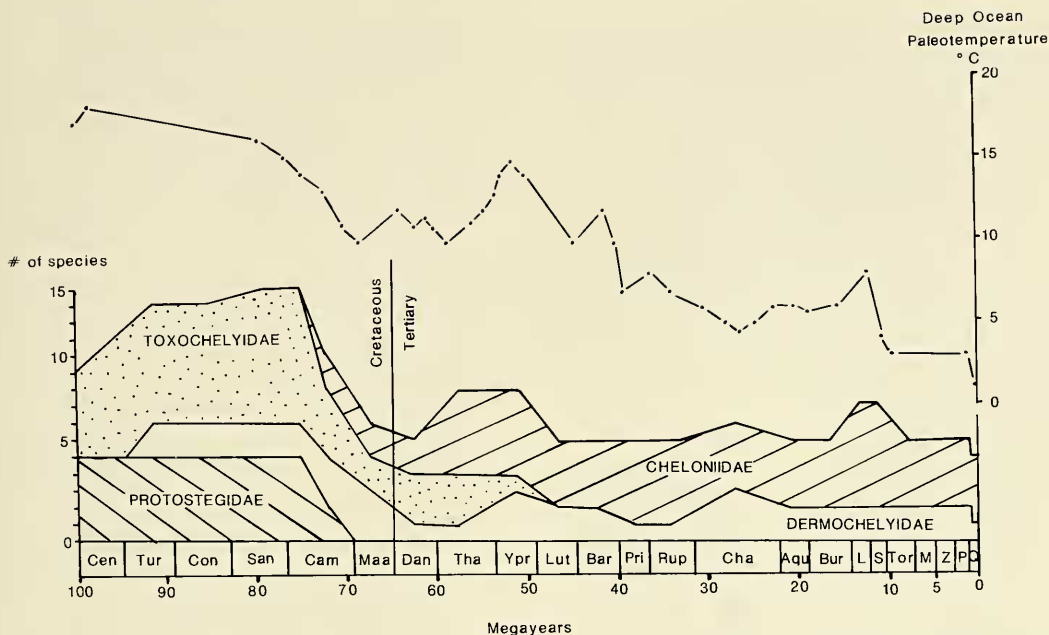
Fig. 27.   Diversity in sea turtle families in comparison with the oxygen isotope derived oceanic paleotem-
perature curve for the northern mid-latitudes (temperature curve adapted from Douglas and Woodruff 1981).
Many factors could explain the strong correlation between ocean temperature and sea turtle diversity, including
(1) increased areal extent of shallow sea habitat during warm spells, (2) more efficient physiology during warm
spells, or (3) better egg viability during warm spells. Cen = Cenomanian, Tur = Turonian, Con = Coniacian,
San = Santonian, Cam = Campanian, Maa = Maastrichtian, Dan = Danian, Tha = Thanetian, Ypr = Ypresian,
Lut = Lutetian, Bar = Bartonian, Pri = Priabonian, Rup = Rupelian, Cha = Chatian, Aqu = Aquitanian, Bur =
Burdigalian, L = Langhian, S = Serravalian, Tor = Tortonian, M = Messinian, Z = Zanclian, P = Piacenzian,
Q = Quaternary undifferentiated.

Generally, however, there has been decline
since the early Eocene to the present diver-
sity of five species worldwide.

Sea Turtles and the
Cretaceous–Tertiary Transition

As indicated by the previous discussion,
sea turtles seem to have had two periods of
exceptional radiation and diversity, once in
the Campanian and once in the Ypresian.
In between those radiations, both the Maas-
trichtian and the Danian represent a time
of exceptionally low diversity. No major ex-
tinction among sea turtles can be localized
at the Maastrichtian–Danian boundary.
Rather, the most dramatic time of extinc-
tion occurs near the end of the Campanian.
This pattern of evolutionary expansion and

contraction does not seem to be strongly
affected either by the recently suggested me-
teoric impact event at the Maastrichtian–
Danian boundary (Alvarez et al. 1980) or
by the more gradual series of climatic and
geologic changes suggested by Officer &
Drake (1983), but does match nicely the
changes in the estimated average oceanic
temperatures for the mid-northern latitudes
through the Late Cretaceous and early Ter-
tiary (Fig. 27). The correlation is so close
that the diversity of sea turtles seems to
have been controlled either directly by av-
erage ocean temperatures around the world
or by the same factors that controlled such
temperatures, rather than by short-term
dramatic events that may have occurred
sporadically throughout geologic time. If

extraterrestrial causes for this extinction are to be invoked, only a large interstellar dust and debris cloud which reduced the intensity of sunlight over an interval of millions of years would fit the pattern observed.

As a generally quiet period in sea turtle history, the Maastrichtian–Danian interval was a time of continuity and stability, marked by neither the radical changes nor great innovations that would occur later in Tertiary. Thus, at a time when many other animal and plant groups have been described as being in a period of massive change or decline, the sea turtles appear to have been essentially unaffected by any great changes taking place around them. As the early Tertiary global warming trend unfolded, the sea turtles concurrently underwent a new evolutionary radiation, undiminished in their evolutionary potential by the Cretaceous–Tertiary transition.

Acknowledgments

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